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The Natural History of Mexican Rattlesnakes

by Barry L. Armstrong
James B. Murphy

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Front cover: The subspecies of the ridgenose rattlesnake *(Crotalus willardi).* Clockwise, starting from the upper left, *C. w. amabilis, C. w. meridionalis, C. w. silus,* and *C. w. willardi.* All photographs by Joseph T. Collins, with the cooperation of the Dallas Zoo.

University of Kansas
Museum of Natural History

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THE NATURAL HISTORY OF MEXICAN RATTLESNAKES

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To Jonathan A. Campbell
for his encouragement

PREFACE

Beginning in November, 1966, studies on rattlesnakes (genera *Crotalus* and *Sistrurus*) and other pit vipers were initiated at the Dallas Zoo which included techniques for maintenance and disease treatments, in conjunction with observations on captive and wild populations. Maintenance techniques and disease treatments have been published in an earlier contribution.

The results of our studies on the ecology and natural history of Mexican rattlesnakes are contained in the present account. Since numerous behavioral sequences were difficult to record in the field, many rattlesnakes were maintained in the laboratory. Over one hundred and twenty-five captive individuals, comprising over 50 taxa (including forms indigenous to the United States) were available for study.

We have attempted to show the value of a multifaceted approach to the study of a body of organisms by beginning with field observations as a basis for understanding, followed by maintenance in the captive state whereupon specimens can be placed upon death in a systematic museum collection. This arrangement allows an investigator to examine various aspects of an animal's "being" by recording data which would be virtually impossible to record in the field. Further, this combined approach maximized our abilities as one of us is somewhat incompetent in the field and the other is an erratic animal keeper.

The assistance and cooperation of many persons contributed to the completion of this study. For various courtesies extended to us, we thank Ray Ashton, James P. Bacon, Robert L. Bezy, Charles M. Bogert, David Brown, Mary E. Dawson, J.S. Dobbs, Michael S. Edwards, Thomas H. Fritts, James C. Gillingham, Ronald Goellner, Harry W. Greene, Herbert S. Harris, Charles Hoessle, Terry Hulsey, J. P. Jones, Thomas L. Jordan, John E. Joy, Tommy Logan, Arthur Lopez, Danny Lopez, Edward Maruska, Hymen Marx, Robert W. Murphy, George R. Pisani, the late Louis Pistoia, Thomas Porter, Steve J. Prchal, Peter C. Pritchard, William F. Pyburn, George B. Rabb, Charles W. Radcliffe, Vincent D. Roth, Thomas Schultz, Hobart M. Smith, Barney Tomberlin, Tom Van Devender, R. Wayne Van Devender, James Walker, Tim Walker, John W. Wright, Richard G. Zweifel, and our many friends throughout Mexico.

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H. Taylor for reading and criticizing the manuscript and offering many helpful suggestions. Photographic assistance was offered by R. Terry Basey, M. Granger, Wayne Seifert, and John H. Tashjian. The able staff of the Dallas Zoo Department of Herpetology, David G. Barker, Raymond K. Guese, William E. Lamoreaux, and Lyndon A. Mitchell have recorded numerous observations and have contributed to the overall maintenance of the rattlesnakes discussed through their enthusiasm and expertise. The librarian staff of Instituto Butantan in São Paulo assisted us in numerous ways. Various persons associated with the University of Texas Press, specifically Ann Hidalgo Manley, Philip L. Wagner, Robert Wauchope, and Robert C. West, allowed us to use figures from *Handbook of Middle American Indians.* Ralph R. Woodiwiss and Anton S. Prechtel of the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, D.C., provided climatic information and allowed us to use material from *Climate of Mexico* by John L. Page. Señor Silvino Aguilar Anguiano, Subdirector Gral. de Geografía y Meteorología, sent climatic data and numerous maps for our use. Members of the Dallas Zoological Society, through the efforts of Bernard Brister, provided partial travel expenses.

The arduous task of typing certain parts of the manuscript was cheerfully accomplished by Kathryn Campbell, Janet Jackson, Martha, F. Murphy, Verna S. Murphy, and Myra Smith. Deb Bennett skillfully executed the drawing of the map of Mexico on the inside back cover.

Finally, special recognition must be extended to Jonathan A. Campbell, who in so many ways aided us in the preparation of this manuscript. His unflagging enthusiasm in the field, the generous donation of specimens under his care, his thoughtful comments and criticisms of the manuscript, his photographic abilities and overall encouragement made the completion of this study much more enjoyable for us. For these reasons, we have dedicated this study to him.

Barry L. Armstrong and James B. Murphy
Dallas Zoo
Dallas, Texas
March 1979

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INTRODUCTION

The view that the central plateau of Mexico was the center of dispersal for rattlesnakes is a zoogeographical position needing no defense (Gloyd 1940, Smith 1946). However, information relating to many species, particularly the primitive montane forms, is limited. There are few observations dealing with the ecology and natural history of Mexican rattlesnakes owing mainly to the inaccessibility of many of the populations. Mexican rattlesnakes inhabit many ecological niches ranging from xeric to mesic environments. One species, *Crotalus triseriatus,* reaches altitudes of 4573 m (Klauber 1956). Many mainland forms are found in the central Mexican plateau where they tend to be restricted to arid, rocky situations. Other species are found in lowland desert habitats, including island populations of the Gulf of California.

The purpose of this study is to: (1) analyze and discuss the environmental components (including physiography, vegetation, and climate) of Mexico and their effect on the distribution of rattlesnakes, and (2) record observations of natural and captive populations.

GENERAL DESCRIPTION OF THE REGION

Information recorded by Goldman (1951) serves to illustrate the physical characteristics of Mexico (Fig. 1). Barbour (1973) presents a detailed description of the central mesa, and Morafka (1977) describes the Chihuahuan Desert. In order to understand the current geological patterns of Mexico and the geohistorical development and paleogeography, the reader is referred to Maldonado-Koerdell (1964) and West (1964). Soil has been treated by Stevens (1964).

The reader should consult such maps as those included in the works of Contreras Arias (1942) and Hernandez (1923) for climatic data. Information on weather and climate is summarized by Vivó (1964). Shreve (1944) discussed rainfall patterns in Mexico, north of the Tropic of Cancer. Refer to Fig. 2 for the mean annual rainfall in Mexico.

Natural vegetation in Middle America is depicted in Fig. 3. Detailed accounts of the vegetational relationships for various Mexican areas are as follows: Beard (1944), Brand (1936, 1937, 1957), Duellman (1965), Eggler (1948), Gentry (1942, 1946a, 1946b), Goldman (1916), Goldman and Moore (1946), Holdridge (1947, 1964), Leavenworth (1946), Leopold (1950, 1972), Lesueur (1945), Lundell (1934, 1942), MacDougal (1908), Martin (1958), Martínez (1945), Miranda (1942, 1952-1953), Miranda and Sharp (1950), Muller (1939, 1947), Nelson (1921), Savage (1960), Sharp (1946), Shreve (1934, 1937a, 1937b, 1939, 1942, 1944), Standley (1920-1926, 1930), Wagner (1964).

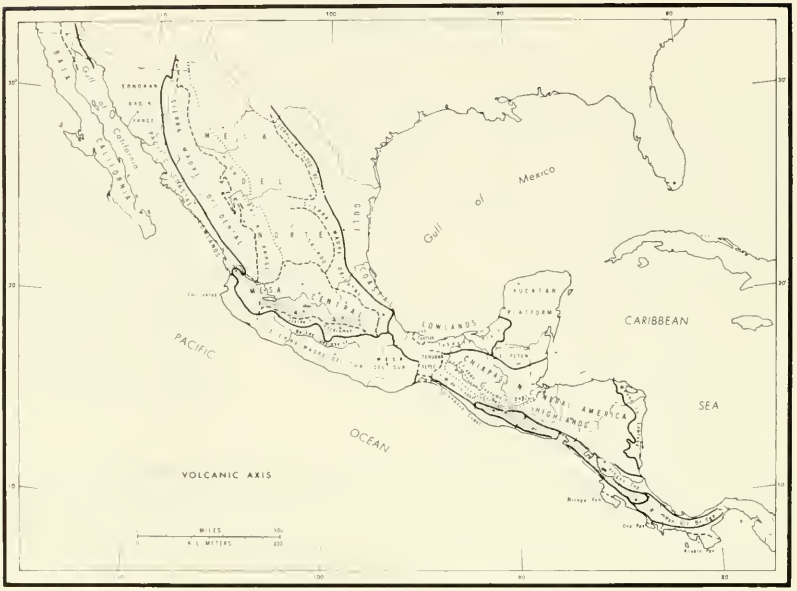

Fig. 1. Physiographic regions of Mexico. Reprinted from *Handbook of Middle American Indians.* Copyright 1964 by Univ. Texas Press. Used by permission of Robert C. West.

Fig. 2. Mean annual rainfall (millimeters) for Mexico. Reproduced by permission from the National Oceanic and Atmospheric Administration, Washington, D.C.

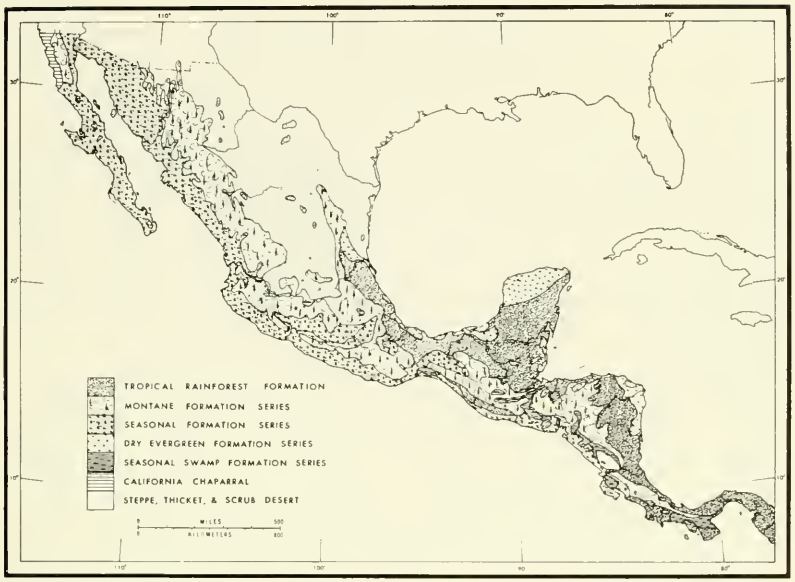

FIG. 3. Natural vegetation of Mexico. Formations classified after Beard and others. Reprinted from *Handbook of Middle American Indians.* Copyright 1964 by Univ. Texas Press. Used by permission of Philip L. Wagner.

MATERIALS AND METHODS

Most of the localities which are listed in the following species accounts are based on our own observations unless otherwise specified, although voucher specimens were not collected in many instances. Since the primary purpose of the study was not to collect rattlesnakes for systematic collections, many of the individuals observed were not collected and in some cases, parturient females were held until they gave birth then released with the young at the same locality. Litters of snakes were not measured and weighed in the field. In the laboratory, weights were recorded with an Ohaus triple-beam balance. Measurements were made on newborn snakes in most cases, using the method described by Quinn and Jones (1974).

Snakes that were removed from wild populations have been deposited (or will be upon their death) in the following vertebrate collections: University of Colorado (UCM), Dallas Museum of Natural History (DMNH), Herbert S. Harris/Robert S. Simmons Private Collection (HSH-RSS), University of Kansas Museum of Natural History (KU), and University of Texas at Arlington (UTA). Each museum number refers to an individual specimen.

ACCOUNTS OF SPECIES

Crotalus atrox Baird and Girard

Crotalus atrox is one of the largest and most aggressive of the Mexican rattlesnakes (Klauber 1972: 448). Although it has been confused with *C. scutulatus* (Klauber 1972: 541), *C. atrox* is generally well known throughout its range. These rattlesnakes are found in a wide variety of habitats at varying elevations. Snakes from southern Oaxaca (Gloyd 1940: 206; Klauber 1952: 102) and central Veracruz (Klauber 1952: 103) present problems in *C. atrox* distribution.

Specimens obtained by us are from the following localities: BAJA CALIFORNIA: Progreso; SONORA: 4.8 km S Sonoyta, Caborca, Esqueda; CHIHUAHUA: 16-32 km S Chihuahua (4 specimens), near El Sueco; NUEVO LEÓN: 16-48 km NE Sabinas Hidalgo (10 specimens).

In Mexico, *C. atrox* inhabits deserts, plains, grasslands, and foothills from near sea level at La Posa, Sonora (Taylor 1936: 497) to at least 2440 m near Alvarez, San Luis Potosí (Klauber 1972: 527). Individuals are generally found in arid country and are not necessarily associated with rocks. Mesquite, dry wash banks, creosote bushes, and burrows provide likely retreats. Taylor (1936: 497) found this snake common along the seashore where shrubs and sandy beaches met. We found *C. atrox* especially plentiful in mesquite grasslands north of Sabinas Hidalgo in Nuevo León. Several snakes have been observed in this area along roads at night during the hot summer months. Hardy and McDiarmid (1969: 213) considered this species to be rather uncommon in the lowlands of extreme northern Sinaloa, and R. T. Basey (pers. comm.) stated that *C. basiliscus* was much more common than *C. atrox* in the nearby Álamos area of southern Sonora. In northern Sonora, near Esqueda, these snakes are not uncommon in sandy, creosote habitats.

Throughout its range, this rattlesnake is mostly nocturnal, at least during the summer months. Most snakes obtained by us have been collected while crossing roads during the early evening. Some individuals have been seen in the early morning or on cloudy days, but they are generally not active and are usually coiled in the mouth of a burrow or under the cover of available brush.

We have observed ritualized combat between males in captivity. Wiley (1929), Hoessle (1963) and Petzold (1963) have discussed reproductive biology and mating behavior in this species. We observed eight *C. atrox* courtship sequences in captivity and a general pattern was apparent. The enclosure in which observations were made measured $80 \times 40 \times 40$ cm high, and the snakes mea-

sured ca. 1.2 m total length. The courtship behavior detailed below was typical for *C. atrox* observations made by us.

0900h The female was placed with the male.
0901 The male sensed her presence and began rapid tongue flicking (1 per sec).
0906 The female responded defensively for a few minutes, but began to react to male.
0911 Male raised anterior third of body 5-6 cm above the surface. Spasmodic jerking of male was apparent throughout entire period (1 every 2 sec) and increased to 1 per sec.
0917 Male started rapid tongue flicking on closest part of body and began to investigate entire lateral and dorsal body surface of female. Jerking of male became more intense (2 per 3 sec). Male held head at 45° angle with mental scale touching dorsum of female. Head of male pressed against dorsum of female, and side-to-side motions (approx. 2.5 cm) were undertaken in clusters (4-5) at irregular intervals.
0927 By moving in an anterior plane, male began to drape large radius coils over female.
0931 Sequence lasted until most of male's body was in contact with female. Male attempted to insert hemipenis but no external eversion of hemipenis was in evidence. Both snakes lifted the tails at the location of the cloacae and occasionally flicked the tails with a side-to-side motion. The substrate was not touched by the tails. Male constantly moved tail in an attempt to align cloacae. When cloacae were juxtaposed, male tried to slide tail under tail of female.
0951 Cloacae were aligned and male inserted. During the latter part of courtship activity, female began twitching with same frequency as male. Jerking and twitching stopped when male inserted. Courtship lasted 20 min and no movement other than steady pulsation of the body near male's tail was in evidence after penetration. Both sexes would occasionally drag each other slowly by the attached hemipenis; this behavior perhaps was initiated by external stimuli.

Actual copulation lasted from 2-8 hours. Breeding dates were recorded from 21 January to 26 January 1974.

Variation of pre-coital behavior was observed on 28 February 1975. During the courtship period, the male was loosely looped over the female and undulated slowly. In addition, the male tried to position his tail under the cloaca of the female. In contrast to the behavior observed previously, the female raised her tail and repeatedly opened her cloaca. When the cloacae were juxtaposed, the male inserted his hemipenis but no external extrusion of the hemipenis was noticed. The male exhibited pulsating throbs (once every 3 seconds) intermittently and the snakes were in copulation nearly 7 hours. The female remained passive throughout the remainder of the sequence. When the snakes were placed in a larger unit ($1.0 \times 0.8 \times 1.2$ m high), the female assumed a vertical anterior trunk posture as the male directed courtship behavior to her. This may be a female rejection posture. Of nine captive litters, two were born in June, one in July, three in August, two in September and one in October. Sexual maturity was reached in 30-36 months.

Litter size varied from six viable young (4 infertile egg masses) to 25 viable young.

Vegetational characteristics associated with the habitat of *C. atrox* in Mexico include the Seasonal Formation Series, the Steppe, Thicket and Scrub Desert as defined by Wagner (1964). Gloyd (1937) and Lowe (1964) described the faunal areas inhabited by this species in Arizona.

Crotalus basiliscus (Cope)

Crotalus basiliscus basiliscus. *Crotalus b. basiliscus* is one of the largest and gentlest of the Mexican *Crotalus*. Gloyd (1940: 161), Bogert and Oliver (1945: 394), and Klauber (1952: 87) have commented on its status in relationship to *C. molossus*. As far as is known, the distribution of these two species usually does not overlap, but Hardy and McDiarmid (1969: 216) gave reasons for believing that the two species live sympatrically in northern Sinaloa. Further investigation is necessary in this area. Klauber (1972) indicates an overlap in the ranges of *C. b. oaxacus* and *C. molossus nigrescens* in Oaxaca. We have found *C. b. basiliscus* to be a common snake (30 specimens) of Mexico's west coast with individuals being observed in tropical thorn forests and, to a lesser degree, in tropical deciduous forests.

Many records of *C. b. basiliscus* are available, no doubt owing to the fact that this rattlesnake is very common. Examples of this snake are known from extreme southern Sonora, south through Sinaloa, Nayarit, Jalisco, Colima, and western Michoacán where its range apparently terminates at the Río Balsas. It would not be surprising, however, to find this rattlesnake on the coastal plain of Guerrero where topographical similarities to its known habitat are apparent. Specimens obtained by us are from the following localities: SINALOA: 4 km S Santa Lucía, 5 km W Concordia; NAYARIT: 4.8 and 8 km E San Blas; JALISCO: 8 km N Ciudad Guzmán, Tamazula; MICHOACÁN: Dos Aguas.

Crotalus b. basiliscus is generally a lowland resident inhabiting the previously mentioned tropical thorn or tropical deciduous forests. Klauber (1972: 528) reported that a specimen from Apatzingán, Michoacán, was collected at 975 m elevation in the arid tropical scrub forest. He felt this to be the upper limits of the altitudinal range of this form, but he was no doubt unfamiliar with the specimen from 19.2 km NE Santa Lucía in Sinaloa (KU 78966) which was collected at 1940 m in a humid pine-oak forest. We can extend the altitudinal limits with a recently collected specimen (UCM 51313) from near Dos Aguas, Michoacán. This snake was found in July 1974, well within the confines of the Sierra de Coalcomán at an elevation of 2225 m. The rattlesnake was located within 3 m of a stream in a canyon bottom in the humid pine-oak forest. Local

residents recognized the individual, but reported that *C. b. basiliscus* was not nearly so common as the abundant *C. pusillus* or the fairly rare *C. durissus culminatus.* Despite the fact that occasional snakes may reach elevations above 2000 m, we consider such occurrences rare, for *C. b. basiliscus* is apparently a lowland form. Most of our specimens have come from below 1000 m in various tropical forests (see Hardy and McDiarmid 1969: 51-58). Another snake (UTA R-6120) was found on the south slope of Cerro Baralosa in the Sierra de Coalcomán. On 21 July 1976, an individual snake (UTA R-6071) was found coiled in shade among rocks at 915 m at Plomosas, Sinaloa, in a transition pine-oak and tropical deciduous forest (Fig. 4). This snake was collected in the same rock slide as an example of *Crotalus stejnegeri. C. b. basiliscus* appears to be most common, or at least most active, during the summer rainy season, and most individuals are located crossing roads. Hardy and McDiarmid (1969: 214) reported that these rattlesnakes had also been found in the dry season in Sinaloa, although this is the period of least activity.

Vegetative components associated with this rattlesnake are the Arid Tropical Scrub Forest (Duellman 1965) and the Tropical Thorn Forest and Tropical Deciduous Forest as defined by Leopold

Fig. 4. Habitat of *Crotalus basiliscus basiliscus, C. lepidus maculosus* and *C. stejnegeri* near Plomosas, Sinaloa, Mexico, September 1976. *Crotalus l. maculosus* occurs in the pine-oak forest covering the top of the bluffs. *Crotalus stejnegeri* and *C. b. basiliscus* are found in the tropical deciduous forest on the lower hillsides and the transition zone at the base of the bluffs. (Photograph by Jonathan A. Campbell.)

(1950). According to Goldman (1951), mesquites, acacias, wild figs, Spanish cedar, palo mulato (probably *Bursera grandifolia*), wild guava *(Psidium guajava), Castilla elastica,* silk-cotton trees and palms grow in the area inhabited by this rattlesnake.

Crotalus basiliscus oaxacus. A Oaxacan subspecies, *C. b. oaxacus*, separated geographically from *C. b. basiliscus* by the entire state of Guerrero, is a rather neglected form from the interior highlands of central Oaxaca. Described in 1948 by Gloyd from two specimens, this subspecies has remained rare in systematic collections. Much of the vegetation in the area once inhabited by *C. b. oaxacus* is now either destroyed or near destruction. This rattlesnake was apparently quite common in the Valley of Oaxaca, but is now rarely encountered there, most individuals now being taken from the mountains surrounding Oaxaca. These mountains exhibit typical pine-oak habitat where rock outcrops are occasionally found, and these areas are superficially similar to the habitat of *C. molossus.* They seem to prefer the more heavily forested areas and, according to the local people, are often seen among rocks where *C. intermedius gloydi* is found. The first specimen obtained by us from El Tejocote (also known as Tejocotes) was located on a steep hillside within the pine-oak forest at 2438 m. We had previously collected in this area rather extensively for three years, and this was the first example of *C. b. oaxacus* we had encountered. A second specimen was secured along the Río Colorado near El Tejocote during the first week in February 1976 at an elevation of 1982 m (J. A. Campbell, pers. comm.). Another was collected on 24 March 1976 in a pine-oak forest at an elevation of 2285 m (UTA R-6820). An individual (UTA R-6060) was found killed on the road on 31 July 1976 at 1030 h in an oak forest (1932 m) at 35.5 km NW Telixtlahuaca.

C. b. oaxacus inhabits the Montane Formation Series and Montane Thicket as defined by Wagner (1964) and Pine-Oak Forest (Duellman 1965).

Crotalus catalinensis Cliff

Crotalus catalinensis is found only on Santa Catalina Island, Baja California del Norte, and is related (ecologically) most closely to *C. ruber lucasensis.* The island is rocky and barren with sparse brush and cacti (Klauber 1972). The temperatures of the coastal islands are similar to the adjacent mainland (Nelson 1921).

One of the male snakes maintained by us, born during September 1975, exhibited head-bobbing and tongue-flicking courtship behavior toward another individual (KU 173096). Another pair copulated on 15 January 1978. This rattlesnake is found in the Seasonal Formation Series and Cactus Scrub as defined by Wagner (1964).

Crotalus cerastes Hallowell

The two subspecies of this rattlesnake that occur in Mexico, *C. c. laterorepens* and *C. c. cercobombus* will be referred to as *C. cerastes,* since their habitats, habits, and behavior are essentially the same. Approximately 300 individuals have been observed by us on the eastern drainage of the Sierra Júarez and Sierra de San Pedro Martír as far south as Puertecitos, a fishing village on the Gulf of California in Baja California del Norte. In Sonora, *C. cerastes* is located north and west of the Nogales-Hermosillo-Guaymas highway (Route 15), with the heaviest concentration of snakes being found in the Desierto de Altar, an arid sandy desert in the extreme northwest part of the state.

Crotalus cerastes generally prefers the sandy areas of its desert environment, although it is not restricted to that particular habitat. Dammann (1961) reported that *C. cerastes* populations may be affected by the amount of vegetation present. In Arizona, the population density of this rattlesnake tended to decrease as the vegetation increased. Too much vegetation may limit the unique locomotor abilities of this species. These rattlesnakes can be found on hard stony terrain, such as the Cottonwood Springs area of Joshua Tree National Monument. These particular individuals are not as common as those found in sandy situations, but they appear to be slightly larger in body girth. This may be due in part to a different diet as mammals rather than lizards are more plentiful in these areas. This terrain also has a more luxuriant growth of desert vegetation. Generally, *C. cerastes* will commonly be found on sandy alluvial fans, sand dunes, sandy washes, and the fringes of desert dry lakes. The greatest concentrations of these rattlesnakes are usually found in areas where wind-blown sand forms small mounds at the bases of creosote bushes (see Brown 1971). Miller and Stebbins (1964) found *C. cerastes* resting under bushes. The areas around San Felipe, Baja California, Yuma, Arizona, and Mexico Route 2 between Mexicali and Sonoyta are good examples of this type of habitat. In these situations, *C. cerastes* is easily located, usually at the mouth of a burrow, or beneath bushes where shade is available. One snake from north of Puerto Peñasco, Sonora, was found in a creosote bush about 30 cm above the sandy soil. This individual appeared to be basking rather than hunting, as the specimen was not alert and did not seem to sense our presence. In these areas the sand shifts constantly and *C. cerastes* is often observed coiled near a bush, partially concealed by sand. Brown (1971) suggested that the unusual cratering behavior serves primarily for thermoregulation and secondarily for concealment during the day, whereas at night the reverse is true. Individuals have also been found within and under the wreckage of dilapidated buildings where as

many as five specimens have been located in one search. This rattlesnake is mostly nocturnal but may be seen during the day in early spring and late fall. Activity cycles seem to be related primarily to thermal considerations (Brown 1971). Moore (1976) suggested that due to circulatory adjustment, tightly coiled, inactive sidewinders (and *C. mitchelli pyrrhus*) were able to conserve heat more effectively than uncoiled snakes. Often, ten or more *C. cerastes* may be encountered by driving roads at night in areas where they are common, with as many as 30 occasionally being seen. Peak activity appears to be late May and early June, particularly in the hours just after sundown. Sidewinders will often coil on asphalt roads where automobiles cause heavy mortality. Brown (1971) felt that the snakes used roads as a source for irradiated heat.

Sidewinders are rather pugnacious and will strike readily. They will often turn and bite when restrained, a characteristic usually associated with montane forms *(C. willardi, C. polystictus).* They prefer a diet of lizards *(Uma, Dipsosaurus, Cnemidophorus, Uta, Crotaphytus)* in captivity, and captive sidewinders will often refuse mice, but readily consume an iguanid lizard. We observed a captive adult female *C. c. cercobombus* feeding on three of her newborn young.

The vegetational regimes inhabited by this species include the Seasonal Formation Series and Cactus Scrub as defined by Wagner (1964). Lowe (1964) described the habitat of this snake in Arizona.

Crotalus durissus Linnaeus

The Neotropical rattlesnakes, *C. durissus,* are among the largest and sometimes most aggressive rattlesnakes indigenous to Mexico. With the exception of an isolated subspecies, *C. d. totonacus* found in Tamaulipas, Querétaro, Veracruz, and southern San Luis Potosí, snakes of the *C. durissus* complex are inhabitants of the country south and east of the Mexican Plateau, including the entire Yucatán peninsula. Despite the fact that the common name given *C. durissus* suggests a jungle inhabitant, these rattlesnakes rarely will be found in such moist places, much preferring savannahs or partially wooded hillsides.

Crotalus durissus durissus. *Crotalus d. durissus* is a resident of the Mexican states of Tabasco, Chiapas, central Veracruz, and southeastern Oaxaca (Klauber 1972). Klauber (1952: 65) cited differences in snakes from near Jalapa and Orizaba, Veracruz, and suggested that with examination of more specimens this population may merit subspecific recognition. *Crotalus d. durissus* has been recorded by us from the following localities: CHIAPAS: 12.8 to 18 km NE Tapanatepec; OAXACA: 19.3 km W Tehuantepec.

This rattlesnake prefers dry savannah habitats with frequent rock outcrops. Hartweg and Oliver (1940) characterized the habitat

of this snake in the vicinity of Tehuantepec as plains. Klauber (1972: 531) suggested that the habitat of *C. d. durissus* was somewhat like that of the arid southwestern United States. Specimens obtained by us from extreme southeastern Oaxaca and southwestern Chiapas were found to be very common in rocky, grassy situations where forests had been partially cleared. In late June, three weeks after the rainy season had begun, individuals were found at night on the road between Tapanatepec and Rizo de Oro. Most were observed on evenings when rains were in the form of light drizzle. *Crotalus d. durissus* ranges from near sea level to at least 1585 m near Comitán, Chiapas (Klauber 1972) and is found in the Tropical Rain Forest as defined by Wagner (1964). According to Goldman (1951), the wild gourd tree, various cacti, *Cassia, Acacia farnesiana, Prosopis juliflora,* two species of *Jatropha, Annona,* two or more species of *Ficus, Ipomoea,* two species of *Pithecollobium,* fan palms and the guásima *(Guazuma ulmifolia)* are found in the area inhabited by this snake.

On 8 December 1976, W. E. Lamoreaux (pers. comm.) introduced an adult male *C. d. cumanensis* into an enclosure (100 × 80 × 75 cm high) containing an adult female *C. d. durissus.* The male initiated head-bobbing movements with rapid tongue-flicking over the female's dorsum. The female remained passive and no intromission was observed. The next day, the pair was *in copulo* at 1300 hours. The coital position of the pair was unusual for although the snakes were firmly joined by the hemipenis, the tails were pointing in directly opposite planes. The male's body pulsated near the vent and the tail was curled upward. During intromission, the male opened his mouth intermittently and began a series of vertical head and neck jerks with occasional tongue flicking. Parturition occurred on 10 June 1977, and produced one dead and nine viable neonates.

Crotalus durissus culminatus. *Crotalus d. culminatus,* a Pacific Coast race, ranges from near sea level near La Placita, Michoacán, and Copala, Guerrero (Wayne Seifert, pers. comm.), to 1982 m near Morelia, Michoacán. These rattlesnakes may reach elevations near 2285 m in the Sierra de Coalcomán where we have seen tanned skins. Local residents have identified live individuals, but this identification should remain tentative until more reliable data are secured. This subspecies occurs from near the Colima border at La Placita, Michoacán, northeast to Morelia, east through southern Morelos and western Puebla to extreme southwestern Oaxaca, including the entire state of Guerrero. Specimens have been recorded by us from: MICHOACÁN: near La Placita, 7 km W Morelia (J. A. Campbell, pers. comm.), Morelia; MORELOS: 5 km W Jojutla.

Crotalus d. culminatus is an inhabitant of rough, rocky, generally arid habitats (Fig. 5). Although Klauber (1972: 530) thought that

FIG. 5. Habitat of *Crotalus durissus culminatus,* near Jojutla, Morelos, Mexico. Open tropical deciduous thorn forest characterized by limestone outcrops. (Photograph by M. Granger.)

this rattlesnake avoided lowland situations, snakes from Copala, Guerrero, and La Placita, Michoacán, have been recorded from near sea level. This lowland habitat can be described as arid tropical scrub forest, characterized by frequent rock outcroppings. Davis and Smith (1953: 141) found *C. d. culminatus* common in lowland mountains south of Tepaltzingo, Morelos, on the northern slopes of the Río Balsas basin. This area is also interlaced with extensive limestone outcroppings. Duellman (1961: 121) commented that 18 specimens from El Sabino, Michoacán, were found near the upper limits of the arid scrub forest (1050 m) on the lower slopes of the Cordillera Volcánica. A specimen from near Morelia, Michoacán, the northern limit of the range of *C. d. culminatus,* was taken on the edge of a lava flow at 1982 m in a mesquite grassland habitat with isolated stands of scrubby oaks. Throughout much of its range, this subspecies is generally nocturnal, and seems to reach a peak period of activity during the summer rainy season, as do most Mexican *Crotalus.* A captive pair was observed copulating on 4 February 1978.

Crotalus d. culminatus inhabits the Arid Tropical Scrub Forest (Duellman 1965) and the Temperate Pine-Oak Forest as defined by Leopold (1950).

Crotalus durissus totonacus. The northeastern subspecies, *C. d. totonacus,* is probably the least studied form of *C. durissus.* Since its description in 1940 (Gloyd and Kauffeld), few specimens have

reached collections, and only recently, with the construction of new roads, has *C. d. totonacus* been observed with some frequency by field investigators. Records obtained by us are from TAMAULIPAS: 48 km N Soto la Marina, 16 km N Aldama. Four subadult individuals were found killed on the road in Tamaulipas: El Carrizo at Kilometer Post 26 on 2 March 1977 (KU 174825), 20.8 km N Soto la Marina on 29 April 1977 (KU 174826), 38.4 km N Soto la Marina on 29 April 1977 (KU 174827), 33.6 km N Soto la Marina (KU 174828). Topographical similarities suggest that *C. d. totonacus* may be found in the state of Hidalgo.

Like most races of *C. durissus, C. d. totonacus* is typically a lowland inhabitant, although specimens have been reported from 1680 m in the lower cloud forest of the Sierra de Guatemala (Martin 1958). Throughout most of its range, the areas inhabited by this snake are either tropical thorn or tropical deciduous forests marked by distinct wet-dry seasons. Two specimens (both juveniles) from east-central Tamaulipas, collected by John E. Joy (pers. comm.) on 7 and 8 August 1975, were found active shortly after dark during rain showers (Fig. 6). A juvenile (UTA R-6707) found killed on the road at Kilometer Post 17 near La Marina Viejo on 2 March 1977 contained rodent hair. *Crotalus d. totonacus* appears to prefer areas around any type of watercourse. Local residents assured us that this is where most of these rattlesnakes were seen, but Dixon *et al.* (1972) found this subspecies in eastern Querétaro at 1585 m in a

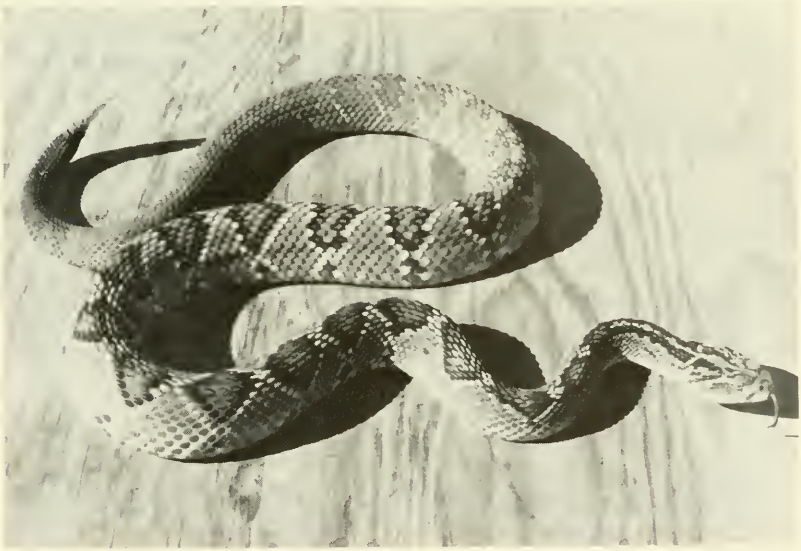

FIG. 6. Subadult *Crotalus durissus totonacus.* Specimen from 48 km N Soto la Marina, Tamaulipas, Mexico. (Photograph by Jonathan A. Campbell.)

pine-oak forest near no standing water. P. Pritchard (pers. comm.) found a large individual on the bank of a small dam. These rattlesnakes are common, but as is the case of most forms of *C. durissus,* the peak period of activity seems to be limited to the rainy season. Growth rates of captive young are the most rapid of any rattlesnake taxa maintained by us.

C. d. totonacus inhabits the Tropical Thorn and Tropical Deciduous Forests, some elements of the temperate deciduous forest as defined by Leopold (1950), and the Seasonal Formation Series and Steppe, Thicket and Scrub Desert as defined by Wagner (1964). The area supports mesquite, huisache, ebony and other shrubs. Along the streams, bald cypresses *(Taxodium)* and cottonwoods are common (Goldman 1951).

L. A. Mitchell and J. E. Joy (pers. comm.) discovered a male *C. d. totonacus* measuring 1.7 m total length, in combat with an adult ocelot, *Felis pardalis,* during February 1977. The animals were below a thick canopy of thorn scrub in early afternoon and the ground beneath the canopy supported little vegetation. A distance of 1.3 m separated the combatants, and the snake was in a defensive posture typical of *C. durissus,* and rattling vigorously. The ocelot remained immobile with the right foreleg raised. When the snake was extended fully with its mouth open after a strike, the ocelot raked with its claws within the snake's mouth, then withdrew the paw before the snake could close its mouth. Later examination of the oral cavity and throat of the snake revealed a number of lacerations in the soft tissue and masseter muscles which were inflicted by the ocelot, but the interstitial skin and scales exterior to the lacerations were not affected. Lacerations were found on the dorsal aspect of the head and neck, but not near the punctures within the snake's mouth or throat. The snake's lower jaw was out of alignment and the mandibular bone was visible when the mouth was open. A large female *C. d. totonacus* was located 15 minutes later, within 12 m of the male. The male rattlesnake was treated for its injuries, but succumbed about two weeks later (KU 174824). The snake regurgitated a large number of ascarids during the two weeks prior to its death.

Crotalus durissus tzabcan. The Yucatán race of this species, *C. d. tzabcan,* unlike *C. d. durissus* and *C. d. culminatus,* is strictly a lowland inhabitant from the Yucatán peninsula, and ranges from eastern Tabasco to include all of Campeche, Quintana Roo, and Yucatán. Neill and Allen (1959, 1960) reported on this rattlesnake in British Honduras.

Crotalus d. tzabcan is quite common throughout the Yucatán peninsula. Duellman (1965: 611) described its habitat as scrub forest with numerous limestone outcrops. Four specimens obtained by us were found between Kantunil and Chichén Itzá, Yucatán,

after 1600 hours (UTA R-5659-60), following a two-hour rainshower.

A male, taken on 18 September 1974 between Kantunil and Chichén Itzá, Yucatán, and a female obtained on 29 August 1969 at Uxmal, Yucatán, were placed together on 11 October 1974. The following observations were recorded by Terry Hulsey (pers. comm.). The female exhibited nervousness and refused to coil near the male. On 24 October she was placed in isolation and again introduced on 7 November. The male shed on 29 December and the female was coiled next to the male for the first time since they were introduced. Courtship behavior was seen on 30 December. The male began rapid head-bobbing and tongue-flicking. He approached the female and tapped her dorsum repeatedly in the vicinity of the 13th and 15th scale rows. The male's activity lasted ca. 30 seconds and he remained immobile for ca. 30 seconds. At the end of each period of activity, the male's tail encircled the female in the vicinity of the vent and he jerked violently. Generally, the head-bobbing motions were directed anteriorly. Pre-coital activity was continued after the male discontinued the cloacal searching motion. The snakes did not copulate. On 2 January 1975 the cage was sprayed with water at 0830 hours and the male began twitching shortly thereafter. The snakes were found *in copulo* at 1500 hours and the male slowly moved his tail in a laterally directed twitching motion. The female was weighed periodically after copulation and the weight increase was as follows: 24 February 1975 (2.1 kg); 20 April (2.6 kg); 12 May (2.7 kg); 25 July (3.0 kg). Twenty-one young (two dead, KU 158547-8) were born on 31 August and were immediately weighed and measured. The range of variation is as follows: total length 290-350 mm, mean 316; weight 18.4-26.8 g, mean 23.4. Other parturition dates are 31 August 1975 (UTA R-6732, 6802), 2 August 1976 (UTA R-6733) and 3 August (UTA R-6734-35). Figure 7 represents one of the young at 35 months.

Crotalus d. tzabcan is found in the Tropical Evergreen and Tropical Rain Forest as defined by Leopold (1950). The area supports *Enterolobium cyclocarpum,* two or more species of *Ficus,* Spanish cedar, logwood, two species of silk-cotton, the chico zapote *(Achras zapota),* palo mulato *(Bursera),* two or more species of *Cassia,* giant nettle *(Urera caracasana)* and Agave (Goldman 1951).

The subspecies of *C. durissus* are very unpredictable in temperament. At times they are aggressive and stand their ground, whereas at other times they are placid. Our specimens have exhibited both of these behavioral extremes. Most *C. durissus* are at least partially nocturnal, and all seem to reach peak activity during the summer rainy season. Young of this species have been collected from late June through late August.

FIG. 7. *Crotalus durissus tzabcan.* See text. (Photograph by Jonathan A. Campbell.)

Crotalus enyo (Cope)

Crotalus enyo, though widespread throughout Baja California, remains biologically neglected in literature on rattlesnakes (Klauber 1931). It is characterized by an unusually small head and rather large rattles, also traits of *C. tigris,* a species not found in Baja California. Races of *C. enyo* are moderately sized rattlesnakes, and throughout much of the range, are lowland or mountain desert dwellers. Van Denburgh and Slevin (1921) found this rattlesnake around human habitations.

Crotalus enyo enyo. The subspecies *C. e. enyo* is a rather common rattlesnake in the Cape region of Baja California del Sur (Fig. 8). Specimens are known from El Mármol, Baja California del Norte, south throughout the peninsula to the southernmost point. Specimens obtained by us were collected at San Antonio (64 km S La Paz) and 14.4 km N Buena Vista (B. Tomberlin, pers. comm.).

Crotalus e. enyo is an inhabitant of arid, rugged deserts and desert mountains throughout its range. Klauber (1972: 531) suggested that snakes found from La Paz to San José del Cabo were from an arid region containing a profusion of cacti, xerophytic shrubs, and rocks. In central Baja California, this rattlesnake lives in association with large boulders, the giant cardon cactus *(Cereus pringlei),* the boojum *(Idria),* and the long-lived elephant tree. B. Tomberlin (pers. comm.) commented that, in the area south of La Paz, this subspecies lives sympatrically with *C. ruber lucasensis*

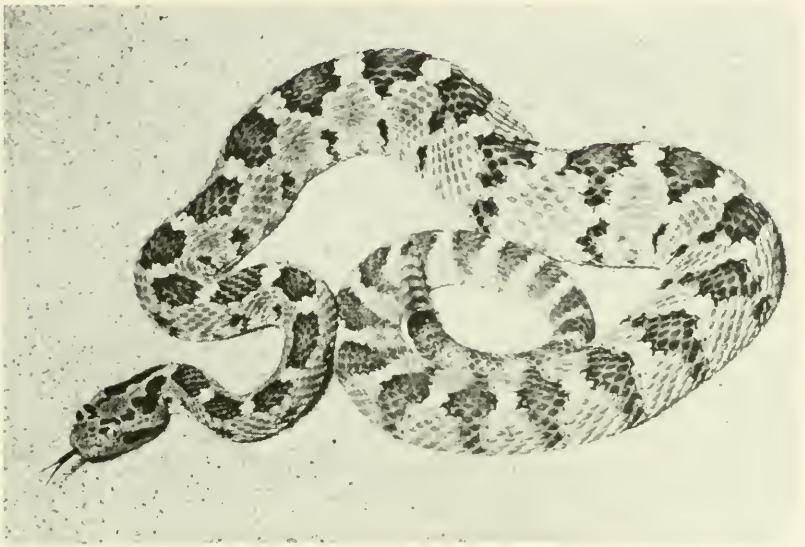

FIG. 8. *Crotalus enyo enyo.* Specimen from 14.4 km N Buena Vista, Baja California del Sur, Mexico. (Photograph by John H. Tashjian.)

and, to a lesser degree, with the speckled rattlesnake, *C. m. mitchelli.* He also stated that specimens of *C. e. enyo* are found in that area from arid flat desert plains to rocky desert mountains.

Crotalus e. enyo is nocturnal for a good portion of the year, and seems to reach a peak activity period in the early fall when southern Baja California receives a fair amount of its annual rainfall. At this time it is commonly found crossing roads at night.

Captive reproduction in *C. e. enyo* has been reported (Tryon and Radcliffe 1977). On 15 January 1975 courtship activity among snakes maintained by us was observed between 1530-1700 hours. The female had just shed and the male rubbed his mental area on the female's dorsum with convulsive forward jerks in the manner of *C. willardi silus* (described later in this paper). During this period the male tried vigorously to thrust his tail beneath the cloacal region of the female, and in some instances, the male's tail completely encircled the female's cloaca. The male would slide forward 1-2 cm by extending his loosely draped coils and bracing his body at the cloacal region of the female. Low intensity twitches accompanied this behavior. Copulation was not observed.

Crotalus e. enyo is an inhabitant of the Seasonal Formation Series as defined by Wagner (1964).

Crotalus enyo furvus. The Rosario rattlesnake, *C. e. furvus,* is a northern form of this species from the San Quintín Plain of the west coast of Baja California del Norte (Lowe and Norris 1954). Until recently, with the completion of a paved road through Baja

California, *C. e. furvus* was known from few specimens, no doubt due to the previously poor road conditions which prevented access to the optimal habitat of this snake.

The San Quintín Plain is characteristic of coastal, open, low-growing scrub habitats in Baja California del Norte. Klauber (1972: 531) described the area as much like western San Diego County, California, but somewhat more rocky and with a lighter brush cover. Lowe and Norris (1954: 57) characterized the area as containing a markedly more mesic climate and biota than the harsh environments both southward and in the interior of the peninsula. The average annual rainfall is about 12.7 cm (Beal 1948), and coastal fog produces some additional moisture in the area. One specimen, obtained by us near El Socorro, appeared to come from a sandy hill where vegetation was sparse, and there was a profusion of coastal ground cover. Many burrows were noted. A specimen collected by R. T. Basey in October 1972 (ambient temperature 21°C) came from a light-colored mud wash where vegetation was extremely sparse (pers. comm.). This specimen was a young adult female which later gave birth to seven young on 26 August 1974. Total length of the young was from 206-222 mm, mean 213. Dennis Bostic (pers. comm.) related that his seven specimens of *C. e. furvus* from near Punta Camalú were collected where two alluvial fans met. Eight additional snakes were taken by one of us (BLA) between 10-15 October 1977 in the vicinity of El Rosario.

Crotalus e. furvus appears to be at least partially nocturnal in that two individuals recorded by R. T. Basey and T. Porter (pers. comm.) were collected on a road at night. The type specimen of this race was taken at noon in the mouth of a small rodent burrow. The Seasonal Formation Series as defined by Wagner (1964) is typical of areas inhabited by *C. e. furvus.*

Crotalus intermedius Troschel

The smallhead rattlesnakes, *C. intermedius,* of southern Mexico remain biologically among the least understood species of rattlesnakes. Little published material on these snakes is available, and few specimens are available in museum collections. Most examples of this rattlesnake are from southeastern Mexico, but Duellman's (1961: 121) record of an individual from Cerro Tancítaro, Michoacán, is indeed unusual. When more field work is done in areas between known localities, the taxonomic status and geographic variation within *C. intermedius* should become more apparent.

Crotalus intermedius intermedius. *Crotalus i. intermedius* has been recorded from eastern Hidalgo, west central Veracruz, and northeastern Puebla (Klauber 1972: 39-40). Pianka and Smith (1959) found *C. i. intermedius* 16-24 km W Japala, Veracruz. A single specimen (KU 155530; Fig. 9) from near Cacaloapan, Puebla,

captured in the summer of 1974 by one of us (BLA), extends the range of this form some 160 km (airline) to the south. This area is at an elevation of 2195 m and is dominated by high desert vegetation where cacti, agave, and yucca are prevalent. A rattlesnake of this race obtained by us was taken at 0995 hours when sunlight was diffused and humidity was high. It was basking in partial shade under a large agave on a southern facing hill. Thunderstorms occurred the previous evening, but the porous limestone soil surrounding the collecting site showed little evidence of moisture. The vegetational habitat preference of *C. i. intermedius* includes the Tropical Evergreen Forest as defined by Leopold (1950).

Crotalus intermedius gloydi. A Oaxacan subspecies, *C. intermedius gloydi* (Fig. 10), is a montane race from the mountains surrounding the city of Oaxaca. To our knowledge it has not been taken from the desert areas of that region. In that respect, it differs greatly from the nominate northern subspecies. Three snakes obtained by us have come from the humid pine-oak forests above 2440 m (Fig. 11) and another specimen (KU 155529) from north of Ixtlán de Juárez at 3020 m. This latter individual was found on a west-facing slope the day following a violent hailstorm which left about 5 cm of hail on the ground. The day it was captured, however, was hot (27°C) and sunny. The snake was found in the shade of an oak that had begun to sprout new foliage after being burned in a fire. J. R. Dixon (pers. comm.) found a specimen of *C. i. gloydi*

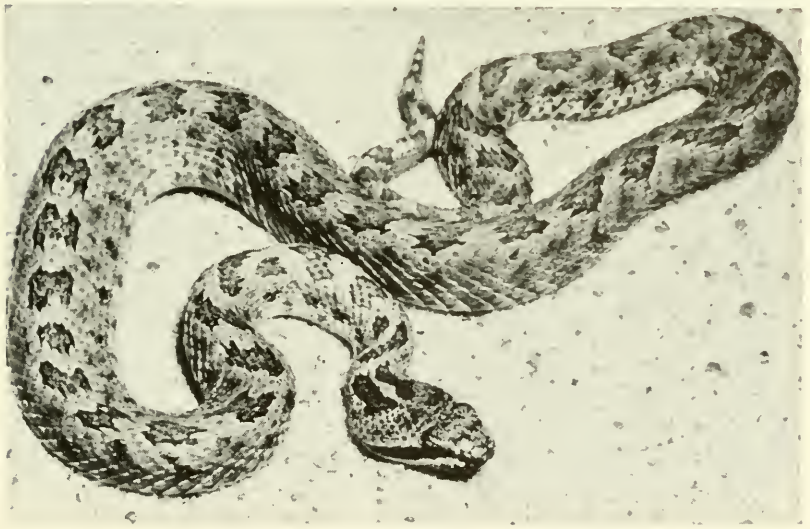

FIG. 9. *Crotalus intermedius intermedius.* Specimen from Cacaloapan, Puebla, Mexico. (Photograph by John H. Tashjian.)

crawling up a vertical stone wall at night in a rainstorm along a highway cut 57.2 km N Oaxaca at 2286 m on 6 June 1956. Other specimens of *C. i. gloydi* collected by us came from near El Tejocote (UTA R-4915, 5627, 5637, 7163), which is northwest of Oaxaca. This area has been extensively logged, and only scattered areas support rattlesnake populations. Six additional specimens were collected in July 1975 from near Cerro Machín (Sierra de Juárez), Suchixtepec (Sierra de Miahuatlán) and El Tejocote (Sierra de Cuatro Venados). Other snakes from the vicinity of El Tejocote are as follows: (UTA R-4915) collected on 20 August 1975, (UTA R-5627) during August 1975 from a pine-oak, madroño forest at 2440 m, (UTA R-5637) during August 1975 in a pine-oak forest at 2285 m, (UTA R-5791-2) on 17 June 1976 in a pine-oak forest at 2285 m, (UTA R-6062-63) on 31 July 1976 in a pine-oak forest at 2285 m, (UTA R-6122) during July 1976 in a pine-oak forest at 2285 m, (UTA R-6229) during August 1976 in a pine-oak forest at 2285 m and (UTA R-6356) during June 1975. We have observed ritualized combat between male *C. i. gloydi* shortly after capture.

The Montane Formation Series and Montane Thicket as defined by Wagner (1964) is characteristic of the habitat of *C. i. gloydi,* and Duellman (1965) listed it as a resident of Pine-Oak Forest. Blue-flowered *Solanum, Ceanothus coeruleus,* wild cherry, and two or more species of oaks and pines are found in the area (Goldman 1951).

Crotalus intermedius omiltemanus. A Guerreran subspecies, *C. i. omiltemanus* (Figs. 12, 13) is probably the most thoroughly studied race of the smallhead rattlesnakes. Most examples of this snake have been taken in the humid pine-oak forests (*Pinus herrerai, P. pseudostrobus, Quercus* sp.) which surround Omilteme in the Sierra Madre del Sur (Davis and Dixon 1957, 1959). Nearly all specimens (35) obtained by us were collected within pine-oak forest (UTA R-4707-10, 6232-33, 6245, 6821); only one individual, collected on 25 May 1975 from 3.2 km W Omilteme, was taken in an area of secondary growth in the adjacent hardwood cloud forest at 2653 m by J. A. Campbell (UTA R-5626). This latter snake may have reached this area via a power line cut. These rattlesnakes also were found only during the major rainy season which usually began in May. This area may receive precipitation every month, but from January to May, it is rather dry. *C. i. omiltemanus* is apparently a rock-dweller, and none of the specimens obtained by us was found any distance from a rocky retreat, with the exception of the cloud forest specimen. In most instances they were found basking on rocks, especially after a rain. One snake (UTA R-2813) was found dead on a grassy hillside on 19 May 1973; cause of death was not determined. We collected snakes from 2075-2592 m, and doubt that these rattlesnakes are found near Chilpancingo which has an

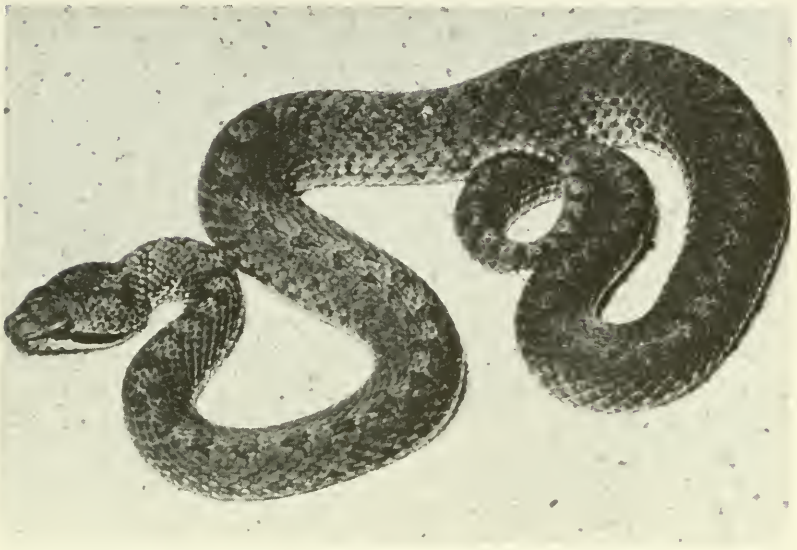

FIG. 10. *Crotalus intermedius gloydi.* Specimen from 31.3 km N Ixtlán de Juarez, Oaxaca, Mexico. (Photograph by John H. Tashjian.)

FIG. 11. Habitat of *Crotalus intermedius gloydi,* pine-oak forest 31.1 km N Ixtlán de Juarez, Oaxaca, Mexico, July 1975. Area had been partially cut and burned the previous year, characterized by epiphytic plants. (Photograph by Jonathan A. Campbell.)

elevation of 1372 m (Klauber 1972: 533). Although *C. i. omiltemanus* has been definitely recorded only from the vicinity of Omilteme, it was to be expected that with additional field collecting other specimens would be secured throughout the upper reaches of the Sierra Madre del Sur. Supportive evidence of this statement is indicated by the collection of a specimen (UTA R-5638) on 28 May 1975 from 1.6 km SW Filo de Caballo by J. A. Campbell. Another adult snake, observed approximately 1 km N Puerto del Gallo (some 60 km WSW Omilteme), escaped before being captured. The elevation at this site was 2950 m, and an example of *Bothrops barbouri* was discovered nearby. Melanistic specimens of *C. i. omiltemanus* were collected in San Vincente, Guerrero (UTA R-4538-9). Five newborn young of this race were found 1.6 km S Omilteme in pine-oak forest at 2286 m on 28 May 1975. Range of variation for length and weight is as follows: total length 194-212 mm, mean 205; snout-vent 182-195 mm, mean 190; weight 4.9-5.4 g, mean 5.2. Ritualized combat between adult males was observed by us among four recently captured snakes.

Campbell (1977) examined the stomachs of 18 *C. i. omiltemanus* from Omilteme, and revealed that these snakes fed almost exclusively on lizards (genus *Sceloporus*) whereas the stomachs of 15 examples of *Bothrops undulatus* from the same area contained mostly rodent remains.

Crotalus lepidus (Kennicott)

The rock rattlesnakes, *C. lepidus,* are typical examples of the various small montane, rock dwelling rattlesnakes inhabiting Mexico. All four subspecies, *lepidus, klauberi, maculosus,* and *morulus,* are generally timid, yet rather irritable and curious at times. Throughout much of the range of *C. lepidus* in Mexico, only limited numbers of specimens have been recorded, probably because the terrain inhabited by these snakes is generally steep, rugged, and inaccessible. More specimens are needed from the southern limits of the ranges to clarify the relationship between *C. lepidus* and *C. triseriatus* (Gloyd 1940: 81).

Crotalus lepidus lepidus. The nominate race, *Crotalus l. lepidus,* is found in pine-oak forests through much of its range, though desert populations are not uncommon. This snake ranges from southeastern New Mexico and Trans-Pecos Texas, south through Coahuila, west-central Nuevo León, eastern Zacatecas, and northwestern San Luis Potosí (Klauber 1972: 62).

Gloyd and Smith (1942: 235) reported a specimen of *C. l. lepidus* from the Sierra del Carmen at 1830 m on an open, southwestern facing slope where junipers were present. Taylor (1952) reported a snake from Cerro Peñon Blanco, San Luis Potosí at 2928 m. The single specimen of this rattlesnake, obtained by us from La As-

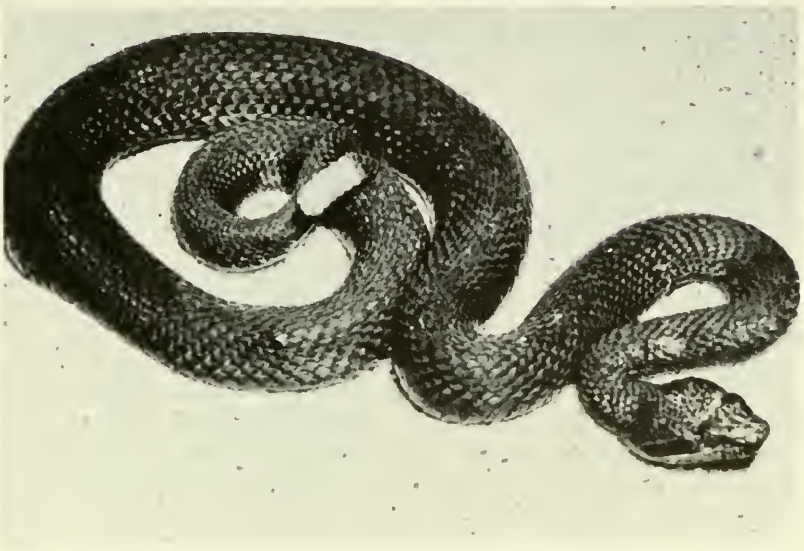

FIG. 12. *Crotalus intermedius omiltemanus.* Melanistic specimen from San Vicente, Guerrero, Mexico. (Photograph by John H. Tashjian.)

FIG. 13. *Crotalus intermedius omiltemanus.* Specimen from near Omilteme, Guerrero, Mexico. (Photograph by John H. Tashjian.)

censión, Nuevo León, was found under similar conditions at 2075 m where junipers, pines, and agaves were prevalent. The specimen, a gravid female weighing 44 g and measuring 435 mm total length (400 mm S-V), appeared to be assignable to *C. l. morulus* according to Klauber (1972: 130) by its having 28 crossbands. However, three of the six young born to this female on 5 June 1974 had fewer than 25 crossbands, and three had 25 or more (one male had 31 crossbands). Range of variation for length and weight for this brood is as follows: total length 165-190 mm, mean 177; S-V 150-173 mm, mean 162; weight 5.0-5.7 g, mean 5.2.

Milstead, Mecham, and McClintock (1950) found *C. l. lepidus* in a persimmon, shin-oak association, and the Scrub Desert as defined by Wagner (1964) is its characteristic habitat. Minton (1959) described the habitat of this race in the Trans-Pecos area.

Crotalus lepidus klauberi. *Crotalus l. klauberi* is normally a resident of moderate elevations in forested mountains throughout most of its range. Snakes from extreme west Texas in the Franklin Mountains are an exception since this mountain range is very arid with little vegetation. Specimens obtained by us are from: CHIHUAHUA: 16 km S Chihuahua, Arroyo Mesteño and Cañon del Alamo in the Sierra del Nido, near Villa Matamoros; DURANGO: near Villa Ocampo.

Most of the data on *C. l. klauberi* obtained by us have been from examples collected in the Chiricahua and Huachuca Mountains of southeastern Arizona. With the exception of the snakes from the Sierra del Nido, Chihuahua, specimens obtained by us from Mexico were collected on roads, and all came from generally the same type of terrain, primarily desert canyons with rock outcrops or ledges, and sparse vegetation. *C. l. klauberi* was collected at elevations from 915 m south of Chihuahua to 1372 m in the vicinity of Villa Ocampo, Durango, where grasses and oaks form a savannah environment. In the Chiricahua, Huachuca, and Sierra del Nido Mountains, *C. l. klauberi* is often located along rocky stream beds, and during the summer rainy season is observed in open pine-oak forests. These rattlesnakes are mostly diurnal, at least in forested mountains, and are most easily observed on warm, humid summer days when they reveal their presence by rattling. Ritualized combat between males of this subspecies has been observed (Carpenter *et al.* 1976). A female specimen, collected at Herb Martyr Dam in the Chiricahua Mountains, Arizona, gave birth to three young on 28 August 1968. Four young were born on 30 August 1975 to another female specimen collected 4.8 km S Madera, Chihuahua, and range of variation for length and weight is as follows: total length 181-196 mm, mean 191; S-V 164-177 mm, mean 172; weight 6.3-7.0 g, mean 6.6. A captive pair of *C. l. klauberi* was observed to breed on 21 February 1977. R. K. Guese (pers. comm.) observed a captive

pair of this race from the Sierra del Nido, Chihuahua, engaged in courtship activity on three occasions between 14-28 September 1977. The male directed rapid head-bobs (3-5/5 sec) on the dorsum of the female. Tongue-flicking occurred at the same speed. The snakes were disturbed after 5 minutes and discontinued the behavior. Another pair of these snakes was observed courting on 11 October 1977, and the male exhibited the same head-bobbing and tongue-flicking behavior (D. G. Barker, pers. comm.).

The Montane Formation Series, Steppe Thicket and Scrub Desert as defined by Wagner (1964) are habitats in which *C. l. klauberi* typically resides.

Jacob and Altenbach (1977) described sexual dichromatism in body coloration in *C. l. klauberi* from New Mexico, Sonora and Chihuahua. Van Devender and Lowe (1977) reported similar sexual dichromatism in this race from Chihuahua. We have seen twelve snakes from Arroyo Mesteño (7 males, 5 females) which exhibit sexual dichromatism. A female gave birth to five young on 18 August 1977. Two male young were only slightly mottled with black speckling and black bands, whereas the two female young were grey, mottled with black speckling and had dark grey bands. The fifth neonate was defective, exhibiting a fusion of the ventral surface in the lower cervical area and the anterior trunk region (UTA R-6946).

Crotalus lepidus maculosus. *C. l. maculosus* (Fig. 14) is a recently described race of rock rattlesnake (Tanner, *et al.*, 1972) whose geographic distribution remains virtually unknown because much of its habitat is inaccessible. It is a resident of the Pacific versant of the Sierra Madre Occidental, and apparently intergrades with *C. l. klauberi* on the high Mexican Plateau in the vicinity of El Salto, Durango.

Where they are most abundant *Crotalus l. maculosus* and another subspecies *C. l. morulus* apparently prefer similar habitat conditions. Both races seem to prefer humid, pine-oak forests with well-defined rainy seasons (Fig. 15). We have unsuccessfully tried to obtain both subspecies in the late spring. However, after the summer rains begin, the two subspecies apparently surface and are quite common. This is unlike many populations of *C. l. lepidus* and *C. l. klauberi,* whose combined distribution divides the ranges of *C. l. maculosus* and *C. l. morulus,* and have adapted in some areas to desert or chaparral conditions. These populations are active above ground throughout the year if the weather is sufficiently warm (24°C). Almost all specimens of *C. l. maculosus* obtained by us were secured under cloudy or partly cloudy conditions, and were particularly common just before and after showers during the rainy season. On 10 July 1973, a female was observed on a southeastern facing rock outcrop 4.8 km W El Alazán, Sinaloa, with eleven young

FIG. 14. *Crotalus lepidus maculosus.* Specimen from Los Bancos, Durango, Mexico. (Photograph by John H. Tashjian.)

coiled or draped about her. This race exhibits behavior typical of all subspecies of *C. lepidus* in that it is alert and quick to seek shelter when discovered. *Crotalus l. maculosus* possesses an unusually small rattle, and it is barely audible even in larger specimens. The accepted technique historically employed to discover *C. lepidus* in its native habitat (by hearing them rattle) is virtually useless when trying to collect this subspecies.

Most of the snakes observed by us, which total forty sightings (KU 155532-534, UTA R-5847), were normally located by exploring southern facing slopes where an abundance of grass and rocks occur in breaks in the pine-oak forest. This subspecies was not found in rock slides as were many *C. l. lepidus* and *C. l. klauberi* populations. However, *C. l. maculosus* is usually found near some kind of rock cover. Lizards of the genus *Sceloporus* appear to be the main food item of this rattlesnake.

Other rattlesnakes found in association with *C. l. maculosus* are *C. p. pricei, C. molossus nigrescens,* and possibly *C. willardi meridionalis* in the eastern part of the range. Some local residents gave positive identification of *C. w. meridionalis* from photographs which we provided.

Crotalus l. maculosus inhabits the Pine-Oak Forest and Pine-Oak Woodland as defined by Leopold (1950).

Crotalus lepidus morulus. *Crotalus l. morulus* (Figs. 16, 17) is the least known of the subspecies of *C. lepidus.* This race was de-

FIG. 15. Habitat of *Crotalus lepidus maculosus, C. pricei pricei* and *C. molossus nigrescens.* Los Bancos, Durango, Mexico. Steep hillsides covered with pine-oak forest. These snakes were most frequently encountered in open areas of rock outcroppings. (Photograph by R. Terry Basey.)

scribed by Klauber (1952: 52) from specimens obtained from P. S. Martin, who collected in the Gómez Farías area of Tamaulipas. Most of the known specimens have been collected in the Gómez Farías area, and an additional specimen is known from Chiche (Martin 1958: 78), which is northwest of Cuidad Victoria, Tamaulipas.

Recently, more snakes of this race have been secured in the Sierra de San Francisco (H. S. Harris, pers. comm.), and we have located an apparently isolated population (19 specimens) in the Sierra Madre Oriental some 24-32 air kilometers northwest of Galeana near the Nuevo León-Coahuila border (KU 159360). No doubt, more *C. l. morulus* will be collected which will fill the present gaps between the few presently known localities.

Most of the rattlesnakes collected by P. S. Martin were located on the humid, eastern slopes of the Sierra de Guatemala at altitudes ranging from 1190-1890 m. These snakes were usually found along the abundant rocky mountain trails in the Gómez Farías area. Pines, oaks, and firs constitute the major vegetational formation of this area, although there is an abundance of agave on the steep rocky sides of the Sierra. Martin (1958) stated that *C. l. morulus* was present in the upper part of the Cloud Forest, but its presence was not confirmed in the Lower Cloud Forest. This area is extremely rugged, and more extensive collecting is needed to delineate the extent of the range of *C. l. morulus.*

FIG. 16. *Crotalus lepidus morulus.* Specimen from near San Antonio de las Alazanas, Coahuila, Mexico. (Photograph by John H. Tashjian.)

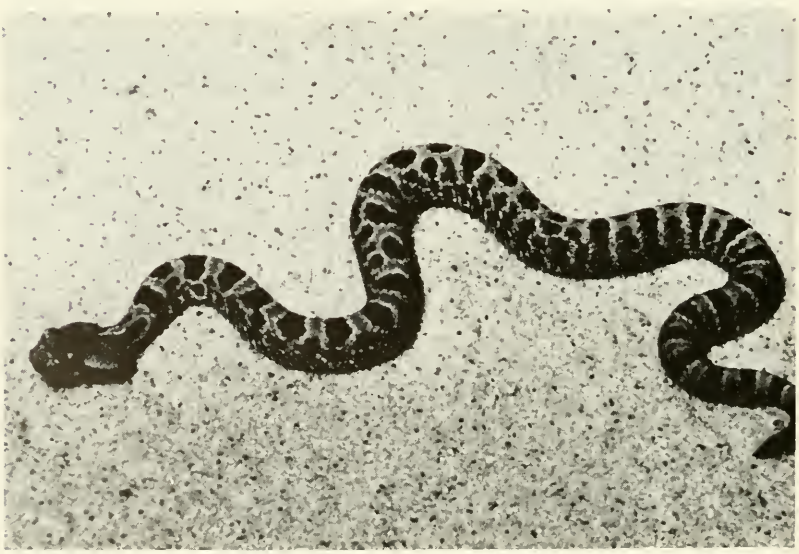

FIG. 17. *Crotalus lepidus morulus.* Juvenile specimen born to female collected near San Antonio de las Alazanas, Coahuila, Mexico. (Photograph by John H. Tashjian.)

In late August 1973, Danial Lopez and one of us (BLA) collected 16 specimens of *C. l. morulus* 24-32 km northwest of Galeana; the specimens ranged from mature adults to newborn young. All were identified as *C. l. morulus* in having at least 28 primary dorsal blotches with the exception of an adult female which had 19 blotches and no mottling. This female gave birth, several days after capture, to four young which had the normal complement of primary blotches, suggesting that the female parent exhibited an aberrant pattern, not uncommon in the *C. lepidus* complex. During summer 1974 an additional individual (UTA R-6123) was taken from the same locality in a pine-scrub oak situation on a steep rocky hillside.

Unlike the specimens collected by Martin which were associated with humid pine-oak forests at the elevations previously mentioned, all of the specimens obtained by us were located at elevations between 2380-2592 m amongst limestone bedrock which had a southern exposure. A few scattered pines and oaks were present, but most of the vegetation consisted of various species of agaves and low growing shrubs, which provided excellent cover for the snakes. These snakes appeared to be extremely common during the only four hours we spent collecting (due to inclement weather) and would often make their presence known by rattling long before we were within their view. They would immediately seek shelter among the rocks and agaves, and several escaped us in this habitat. Captured snakes defended themselves vigorously and often bit themselves or the tongs that were used to secure them.

This subspecies has been reported from the Humid Pine-Oak Forest to Pine-Oak Forest (Martin 1958).

Crotalus mitchelli (Cope)

The speckled rattlesnake, *C. mitchelli,* is an inhabitant of the American Southwest, Baja California, islands in the Gulf of California, and one island, Santa Margarita, off the Pacific coast of Baja California del Sur (Klauber 1972). It is a highly variable rattlesnake, both in size and color, and to a lesser degree in pattern. Color and pattern seem to be correlated with the general color of the rocky terrain which any given population inhabits.

Crotalus mitchelli mitchelli. The San Lucan subspecies, *C. m. mitchelli*, ranges from the southern border of Baja California del Norte, south throughout the peninsula. Island populations are located on Cerralvo, Espírito Santo, San José, Carmen, and Santa Margarita Islands (Klauber 1972). The range does not include Santa Cruz Island (Soulé and Sloan 1966). This rattlesnake is common throughout its range, but is most easily observed in the Cape region. Klauber (1936) recorded specimens from Cape San Lucas, San José del Cabo, Miraflores, Todos Santos, La Paz, Mulegé,

Santa Rosalia, and San Ignacio. Specimens obtained by us are from 8 km N San José del Cabo and 16.1 km N Buena Vista (KU 173097).

Crotalus m. mitchelli is a dweller of the rocky portion of Baja California. Rarely will it be found any distance from rocky retreats, and it seems to prefer rocky canyons and rock outcrops (B. Tomberlin, pers. comm.). This rattlesnake has, however, been found on desert flats where desert shrubs and burrows provide shelter. *Crotalus e. enyo* and *C. ruber lucasensis* are often found sympatrically with *C. m. mitchelli,* although the first two are not as prevalent in rocky situations. Klauber (1972: 536) found that *C. m. mitchelli* was a rock dweller, but also indicated it was found in brushy areas. Most of these rattlesnakes are nocturnal, since temperatures in southern Baja limit diurnal activity. Activity reaches peak periods during the late summer rainy season. These rattlesnakes are most often observed at night as they are crossing roads.

A captive pair of *C. m. mitchelli* was observed *in copulo* on 13 October 1975 at 0800 hours. The right hemipenis of the male was inserted, and a prominent bulge was evident which extended ten scale rows anterior to the vent of the female. The snakes separated at 1500 hours. On 29 June 1976 the female gave birth to one neonate and one infertile egg mass. The newborn snake measured 275 mm in total length, S-V 263 mm, weight 17.5 g (UTA R-6939).

The Seasonal Formation Series and Cactus Scrub and Savannah as defined by Wagner (1964) are typical vegetative regimes inhabited by *C. m. mitchelli.* These areas support mesquite, creosote bushes *(Larrea),* cacti and other arid vegetation (Goldman 1951).

Crotalus mitchelli pyrrhus. A southwestern subspecies, *C. m. pyrrhus,* is a rock-dwelling rattlesnake that ranges in Mexico from the California border to the southern portions of Baja California del Norte. This rattlesnake is common on the desert portions of the Sierra Juárez and Sierra de San Pedro Mártir. It is also found on the western slopes in chaparral situations, but not commonly. Two rattlesnakes obtained by us from south of Puertecitos were found in the vicinity of abandoned sulphur mines in extremely rocky mountains. They were found just after sundown in early spring, a period of the year that seems to be a peak activity time for *C. m. pyrrhus.* We have observed many individuals of this subspecies north of the U.S. border in southern San Diego County, California, during early spring. Fewer specimens were found during summer and fall. To take advantage of favorable ambient temperatures, this rattlesnake shifts from a diurnal mode of activity in the spring and fall to nocturnal activity in the summer (Moore 1976).

Crotalus m. pyrrhus inhabits the California Chaparral, Seasonal Formation Series, Cactus Scrub, and Montane Thicket as defined by Wagner (1964).

Crotalus mitchelli muertensis. A dwarf subspecies, *C. m. muertensis,* is an insular form of *C. mitchelli* from El Muerto Island of the San Luis group in the Gulf of California. El Muerto is the second largest island in the group, is found ca. 6.4 km southeast of Huérfanito Island (the northernmost island in the San Luis group), and is an extremely arid, rocky island supporting sparse vegetation. During the summer, temperatures on the island reach high extremes and limit reptilian activity.

Sixteen specimens obtained by us (KU 155535, 174830) were taken from the western and southwestern portions of the island on 30 May 1969 between 1000-2000 hours; most were released after capture. The majority of these specimens were found shortly after sunset, since daytime temperature reached approximately 38°C. Several specimens were found within 3 m of the water, foraging in beach debris. Other specimens were located on rocks, and some were found under sparse bushes. A single specimen was recorded at 183 m elevation. Two lizards, *Uta stansburiana* and *Streptosaurus mearnsi,* as well as a species of *Peromyscus,* occur on the El Muerto Island in large numbers, and probably make up a sizable portion of the diet of *C. m. muertensis.*

These dwarf rattlesnakes would rattle long before we were within 6 m of them, indicating a high degree of alertness. Several individuals escaped under massive rockpiles before we were able to observe them. Those captured resisted vigorously, and all thrashed violently. Although all were observed before sundown, it is reasonable to assume that *C. m. muertensis* is mostly nocturnal because of excessively high daytime temperatures.

Two of the snakes captured by us bred in captivity on 23 March 1977. At the time of collection, the male measured 355 mm, and the female 280 mm, in total length. At the time of breeding, the male measured 680 mm, and the female 610 mm, in total length. Two live and two dead young (UTA R-7218-19), and three infertile masses, were born on 13 September 1977. Total length of the four young, measured and weighed eight days after birth, was 143-179 mm (mean 167) and weight was 3.3-7.0 g (mean 4.9).

Crotalus m. muertensis inhabits the Seasonal Formation Series and Cactus Scrub as defined by Wagner (1964).

Crotalus molossus Baird and Girard

The blacktail rattlesnakes, *C. molossus,* of the American southwest and the central plateau of Mexico, are well known throughout their range despite the fact that they were at times confused with *C. basiliscus* (Gloyd 1940: 161; Klauber 1952: 87). Large collections

of the subspecies *C. m. molossus* and *C. m. nigrescens* have been made in past years, and only *C. m. estebanensis,* from San Esteban Island in the Gulf of California, remains biologically unknown. All three subspecies of *C. molossus* attain moderate size, and specimens of *C. m. molossus* and *C. m. nigrescens* are among the most handsome rattlesnakes we have had the opportunity to observe. This rattlesnake appears to be adaptively successful; the range and variety of habitats within its area of distribution are unsurpassed by most other Mexican rattlesnake species.

Crotalus molossus molossus. *Crotalus m. molossus* lives in diverse habitats from the Edwards Plateau in west-central Texas through Arizona to the Grand Canyon. In Mexico, *C. m. molossus* has been reported from the states of Sonora, Chihuahua and Coahuila; it intergrades with *C. m. nigrescens* in the southern portion of its range. See Klauber (1952: 91) for a discussion of intergradation in this species. Specimens obtained by us have been recorded from: SONORA: 4.8 km S Sonoyta; CHIHUAHUA: the Sierra del Nido complex, 16 km S Chihuahua. We have observed approximately 30 individuals.

Although somewhat unspecialized ecologically (Dammann 1961), *C. m. molossus* is generally considered a montane species, preferring rocky retreats within dominant pine-oak forests. Typical habitat niches for this rattlesnake from mountain ranges such as the Chiricahuas and Huachucas in southern Arizona, and the Sierra de Ajos and Sierra del Nido of northern Mexico, reflects this preference. This snake is often observed at high elevations (up to 2592 m) in the Chiricahua Mountains of Arizona. However, it appears to be more common below 2135 m on southern or southeastern facing slopes of the Chiricahuas where oak, madroño, agave, and various grasses are the dominant vegetation. Pough (1966) observed many in the talus rockslides where *C. lepidus klauberi* is quite common and our observations corroborate those made by him. Rocky stream beds are also inhabited by *C. m. molossus,* especially during the summer rainy season. *C. m. molossus* is not restricted to forested mountains, however, as Klauber (1972: 537) cited specimens from the valleys and plains of Cochise County in Arizona which average ca. 1220-1525 m elevation. We have observed this subspecies in desert situations north of Scottsdale, Organ Pipe National Monument, and near Gates Pass, south of Tucson, Arizona. Taylor (1936: 497-498) found *C. m. molossus* to be common in rocky habitats northwest of Guaymas at La Posa, which is near sea level. Perhaps the most unexpected place where this snake has been found is the sand dunes south of Cuidad Juárez in Chihuahua, where a specimen was taken by T. Walker (pers. comm.).

Most *C. m. molossus* are gentle in disposition and generally seek escape when approached. They rarely rattle, although those found

in rockslides will at times reveal their presence by rattling, a characteristic they share with *C. lepidus* and *C. pricei.* Allen (1933) found *C. m. molossus* in trees ca. 2 m above the ground.

C. m. molossus inhabits the Seasonal Formation Series, Montane Formation Series and Scrub Desert vegetational classifications as defined by Wagner (1964). See Gloyd (1937) and Lowe (1964) for a description of the habitat of this race in Arizona.

Crotalus molossus nigrescens. The Mexican blacktail rattlesnake, *C. m. nigrescens* (Fig. 18), is generally a resident of temperate pine-oak forests of the central plateau of Mexico, and Gloyd (1940: 164) listed localities for every state within the plateau. We have observed twenty snakes from the following localities: DURANGO: 17 km N Las Nieves (UTA R-5630), 16 km W Durango, Los Bancos, 8.3 km E Coyotes (UTA R-5700), La Ciudad; JALISCO: W Zacoalco; MICHOACÁN: 4.8 km S Carapan, Contepec, 7 km W Morelia, Morelia (UTA R-5112-4), Tacícuaro; MORELOS: the lava beds off the toll road between Mexico City and Cuernavaca; VERACRUZ: the lava beds near Perote.

Crotalus m. nigrescens does not occupy as many varied habitats as *C. m. molossus,* but is not restricted to a specific environment. Individuals were observed by us near Las Nieves, Durango, in rock outcrops at 1220 m within an oak-grass savannah. They were common there, and the local residents were well aware of their presence. The other previously listed locales in Durango were typically pine-oak situations where broken rock and various grasses provided

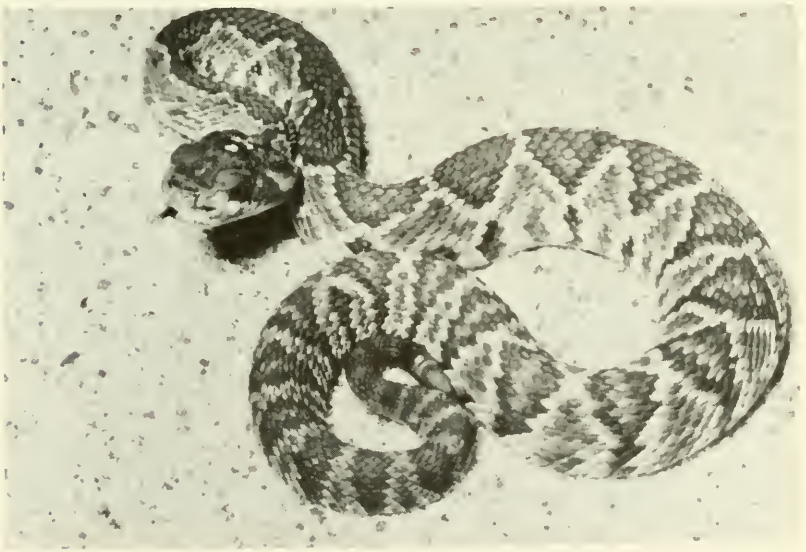

FIG. 18. *Crotalus molossus nigrescens.* Specimen from near Morelia, Michoacán, Mexico. Juvenile. (Photograph by John H. Tashjian.)

excellent cover and a varied food supply (Fig. 15). Most of the rattlesnakes observed by us from these areas in Durango were found basking in the late morning during the July-August rainy season. Those from Carapan, Michoacán, Perote, Veracruz, and north of Cuernavaca, Morelos, were all located in lava bed areas. Davis and Smith (1953: 141) thought that the occurrence of *C. m. nigrescens* in Morelos was doubtful based on geographic grounds. At Carapan in Michoacán they were extremely common (10 observed). The specimens from Tacícuaro and Contepec, Michoacán, were in mesquite grassland, a habitat in which Klauber (1972: 538) had previously speculated that this subspecies might occur. J. R. Dixon (pers. comm.) found a specimen in sweet-gum, oak forest on the east-facing slope of Sierra Madre, 11.2 km ENE Pinal de Amoles, Querétaro, at 1981 m elevation.

Dunkle and Smith (1937) found a female *C. m. nigrescens* with 16 young in a canyon west of La Colorado, Zacatecas. Copulation was observed by us between a captive pair on two occasions (28 May 1973 and 2 March 1974); no pulsations or other movements were noticed. No young were born from these observed unions, but on 9 June 1975 five young were born in captivity, and were weighed and measured. Range of variation is as follows: total length 291-316 mm (mean 304); S-V 267-290 mm (mean 284); weight 25.4-27.9 g (mean 26.6).

Two *C. m. nigrescens* were observed copulating on 1 February 1978 at 0920 hours. The diameter of the female's cloaca was 15 mm and was distended due to the male's hemipenis. A noticeable bulge in the female's body extended 35 mm anterior to her cloaca. The shoulder spines of the hemipenis were visible and the organ was dark purple in coloration. Coitus lasted 105 minutes and detumescence of the hemipenis occupied 100 seconds. Intermittent head-bobbing and tongue-flicking sequences by both snakes occurred during coitus.

An open mouth defensive posture was observed in three individuals. The mouths were held open for over five minutes when the snakes were provoked.

The subspecies *C. m. nigrescens* inhabits the Temperate Pine-Oak Forest as defined by Leopold (1950) and Mesquite Grassland (Klauber 1972).

Crotalus polystictus (Cope)

Previous accounts of *Crotalus polystictus* indicated a preference for marshy situations and this snake was generally referred to as the "aquatic rattlesnake." This presumed preference for aquatic situations was reinforced by specimens, captured in 1919 by Paul D. R. Ruthling, which were secured in the tules of Lake Chapala, Jalisco (Klauber 1956). However, this was probably an unusual

situation since Ruthling pointed out that this area was, at the time of collection, a flooded swampland. In this ephemeral environment, it is easy to understand why so many specimens (20-25) were observed by Ruthling, and also why the species was thought to prefer an aquatic habitat. It is unlikely for a snake with a warning mechanism such as a rattle to live in aquatic situations where the rattle would be rendered useless.

In recent years we have captured or observed over 100 specimens of *C. polystictus* in the vicinity of the Nevado de Colima in southern Jalisco (Fig. 21) and northern Michoacán. Smith and Higareda (1965) commented on specimens from this area. In Jalisco, this snake has been found on plateaus which occur in breaks in the pine-oak forest at elevations of 2075-2317 m. Often these areas are interlaced with gently flowing streams. This rattlesnake can be found during most months of the year; we have records from December, February, and May through September. Snakes obtained by us are from the following localities: JALISCO: near Chapala (UTA R-4000), Rancho San Francisco (UTA R-4499, 4906-8, 4916, 5666-7, 6043, 6250, 6704, 6822-23, 6927; Figs. 19, 20); MICHOACÁN: Tacícuaro (KU 155540-541), 8 km W Morelia, 18 km W Jiquilpan, 5 km N Cato de las Esperanzas.

Most *C. polystictus* are found in rocky situations with an abundance of tall grass called *zacatón*. None of these rattlesnakes have as yet been discovered in pine-oak forest, but they may occur in that habitat. In Michoacán, near Tacícuaro, *C. polystictus* has been

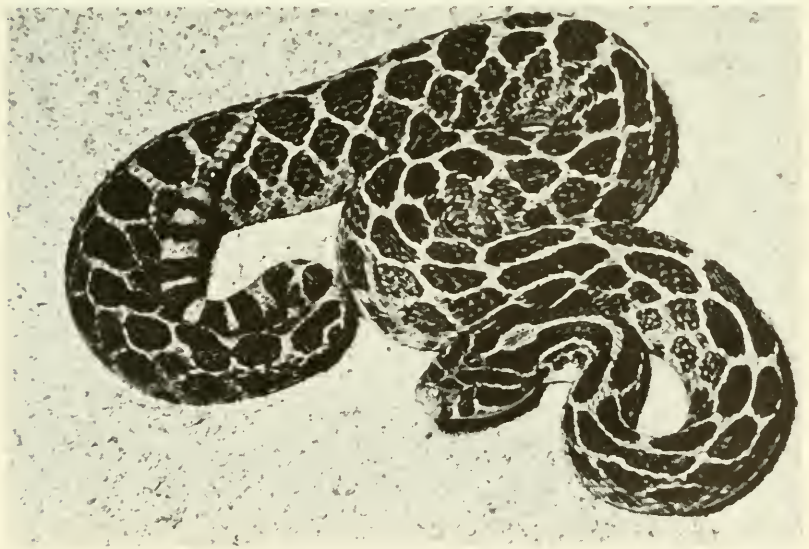

Fig. 19. *Crotalus polystictus*. Specimen from Rancho San Francisco, Jalisco, Mexico. (Photograph by John H. Tashjian.)

FIG. 20. *Crotalus polystictus.* Juvenile specimen born to female collected at Rancho San Francisco, Jalisco, Mexico. (Photograph by John H. Tashjian.)

FIG. 21. Habitat of *Crotalus polystictus.* Rancho San Francisco, Jalisco, Mexico. Snakes were commonly found among boulders or in gopher burrows in grassy meadows with surrounding pine forest on hillsides. (Photograph by M. Granger.)

collected in mesquite grassland (Duellman 1965: 655). This area has rocky outcrops where the species is easily located. We have also collected this species in plains-grassland areas, although it does not appear to be abundant in this environment.

Crotalus polystictus is found rather commonly in late spring when summer rains have not yet been sufficiently heavy to contribute to growth of grass cover. During this period, they become somewhat nocturnal, active individuals having been recorded as late as 2200 hours. In late spring, *C. polystictus* displays a rather mild disposition and is usually quite inoffensive. Some specimens have been observed attempting to hide their heads beneath a coil of their body, behavior similar to that exhibited by *Lichanura trivirgata roseofusca.* During the summer, this species becomes much more aggressive and will generally not retreat when approached. We observed an individual which, upon discovery, opened its mouth in a threatening pose similar to the behavior exhibited by *Agkistrodon piscivorus. Lampropeltis triangulum arcifera,* a harmless colubrid snake, is common in the vicinity of the Nevado de Colima, and may be an important predator upon these rattlesnakes.

The known range of *C. polystictus* is decreasing due to habitat destruction. The plateados inhabited by these rattlesnakes are being altered for agricultural use because they are more easily cleared than adjacent pine-oak forests.

The preferred habitat of *C. polystictus* is Temperate Pine-Oak Forest as defined by Leopold (1950), and Mesquite Grassland (Duellman 1965).

Cuesta Terron (1930-31) reported on a brood of 14 newborn young whose average total length was 12 cm, a figure considerably smaller than the mean total length of broods measured by us. It is possible that Cuesta Terron may have misidentified his snakes (see Fig. 6, p. 54), although we have not seen his specimens.

Data are available to us for six broods born to females of this species, as follows: Female A, weighing 111 g and measuring 608 m total length (575 mm S-V), gave birth to ten young on 20 June 1974: total length 200-223 mm, mean 211; S-V 184-208 mm, mean 195; weight 6.3-10.9 g, mean 7.2. Female B, weighing 166 g and measuring 660 mm total length (620 mm S-V), gave birth to twelve young on 13 June 1974: total length 211-287 mm, mean 222; S-V 198-271 mm, mean 208; weight 8.5-11.5 g, mean 9.9. Female C gave birth to seven young on 26 June 1975: total length 198-232 mm, mean 216; S-V 185-211 mm, mean 200; weight 9.9-10.5 g, mean 10.1. Female D gave birth to seven neonates on 30 June 1975: total length 182-205 mm, mean 197; S-V 167-185 mm, mean 179; weight 9.9-11.1 g, mean 10.6. Female E gave birth to five stillborn young on 30 June 1975: total length 155-203 mm, mean

177; weight 2.4-5.5 g, mean 4.0. Female F gave birth to seven young on 25 June 1975: total length 227-239 mm, mean 232; S-V 201-219 mm, mean 212; weight 9.5-10.9 g, mean 10.2. The range of variation of the six broods is as follows: total length 155-287 mm, mean 214; S-V 167-271 mm, mean 201; weight 2.4-11.5 g, mean 8.9. Two of the snakes born to Female A were maintained in captivity and exhibited courting behavior on 31 January 1978.

Crotalus pricei Van Denburgh

Crotalus pricei pricei. *Crotalus p. pricei* (Fig. 22) is the more commonly known subspecies of this snake, large collections having been made in Santa Rita, Huachuca, Chiricahua, and Graham Mountains of southeastern Arizona. Fewer individuals of this race have been recorded from Mexico, yet they are rather abundant in Mexico in pine-oak forests at elevations ranging from 2135 to at least 2745 m. We have observed these rattlesnakes from the following localities in Mexico: SONORA: Sierra de Ajos (UTA R-6931-34); CHIHUAHUA: the Sierra del Nido complex; DURANGO: Las Adjuntas, near Coyotes, 14 km ENE El Salto (UTA R-2021), Llano Grande (KU 158561), Los Bancos (UTA R-6251). Klauber (1972: 45) suggested that *C. p. pricei* may also occur in eastern Sinaloa and northern Nayarit, but to our knowledge, no specimens have been secured in either of these states.

Crotalus p. pricei is a resident of high rocky pine-covered slopes (Fig. 23). In the United States, it seems to prefer talus rock slides

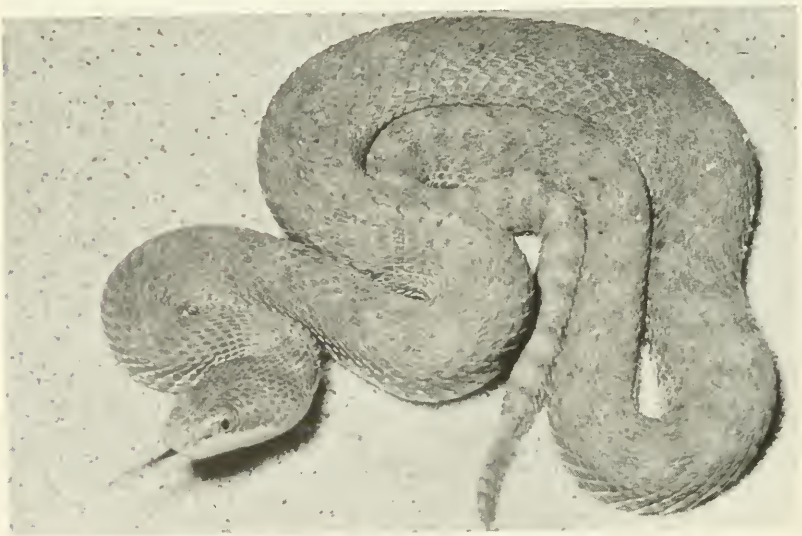

FIG. 22. *Crotalus pricei pricei.* Specimen from near Los Bancos, Durango, Mexico. (Photograph by John H. Tashjian.)

in the previously mentioned mountain ranges. This rattlesnake will often divulge its presence by rattling when approached. However, like many of the montane rattlesnakes, *C. p. pricei* is curious and usually retreats only a short distance. Although generally associated with rocks, this rattlesnake may be found also in grassy mountain valleys where prey, such as lizards and small rodents, is abundant. One adult snake (UTA R-2021) contained a juvenile lizard *(Sceloporus poinsetti).* We have frequently observed this subspecies on warm, humid days when diffused sunlight is prevalent. Individuals were collected near rocky retreats from March to November, even when a light snow cover was present. No doubt these retreats are the warmest micro-habitats available to this rattlesnake in mountains. On 17 March 1965, two *C. p. pricei* were found on a south-facing talus slope at Barfoot, sometimes known as Buena Vista Peak, Chiricahua Mountains, Arizona at 1220 hours. Snow surrounded the talus slope, and the ambient temperature was 11°C.

In Mexico, *C. p. pricei* is probably the most common rattlesnake at higher elevations within its range, where it is found sympatrically with *C. willardi, C. lepidus,* and *C. molossus.* We have collected *C. p. pricei* from May through September, sometimes under the most adverse weather conditions. In June 1973 we secured four individuals on a south-facing slope near Los Bancos, Durango (Fig.

Fig. 23. Habitat of *Crotalus pricei pricei* and *C. willardi meridionalis.* Sparse pine-oak forest near Llano Grande, Durango, Mexico. *Crotalus p. pricei* was generally discovered in rocky areas while *C. w. meridionalis* was collected in thick grass or underbrush, mainly manzanita and scrub oak, on hillsides. (Photograph by Lyndon A. Mitchell.)

15), two hours after a driving hail storm. The hail melted quickly and all four snakes were active, apparently foraging for food. These four snakes exhibited an unusual array of body patterns. One individual had the typical coloration of a slate-gray background with brown dorsal spots. The second example exhibited a blue-gray background with rusty colored spots. The third specimen was overall salmon-pink with tan spotting, and the fourth snake was a completely patternless light tan. These four specimens were captured within a 45 m radius.

A female specimen of *C. p. pricei* obtained at Los Bancos, Durango, gave birth to three young on 24-28 July 1973. Another female, taken near Onion Saddle, Chiricahua Mountains, Arizona, gave birth to four young on 20 May 1967. Three young *C. p. pricei* were found on 11 July 1973 near Los Bancos, Durango, in a rock crevice; they had not shed. A captive mating produced four young on 9 July 1971 (J. A. Campbell, pers. comm.). Three of the four young were born alive and weighed 2.7, 3.9, 2.4 g; mean 3.0. Four female specimens from Llano Grande, Durango, gave birth in the laboratory on 10, 14, 27, and 29 July 1977, respectively. Data on these four broods is as follows: Female A produced eight young (2 stillborn, less than 50 mm total length), total length 157-167 mm, mean 164; weight 4.0-4.2 g, mean 4.1; Female B gave birth to nine viable young (four died within two days, UTA R-6935-8), total length 152-173 mm, mean 162; weight 3.5-4.0 g, mean 3.6; Female C gave birth to six viable young, total length 159-169 mm, mean 162; weight 5.1-5.6; Female D produced six young, total length 160-185 mm, mean 168; weight 3.6-3.9 g, mean 3.7. The range of variation and mean for all litters was as follows: total length 152-185 mm, mean 164; weight 3.5-5.6 g, mean 4.1. All but one of the females were collected while basking in the early morning on rocks (L. A. Mitchell and D. G. Barker, pers. comm.). Kauffeld (1943a, 1943b) reported that an example of *C. p. pricei* collected at Barfoot, Buena Vista Peak, Chiricahua Mountains, Cochise County, Arizona, gave birth to six young on 19 August. He cited another record of a brood of this race born on 3 August 1941. Keasey (1969) recorded a birth of eight young on 23 September 1953. Six young were born on 19 July 1971 to a female secured at Los Leones, Chihuahua (Van Devender and Lowe 1977).

C. p. pricei inhabits the Temperate Pine-Oak association as defined by Leopold (1950). See Gloyd (1937) and Lowe (1964) for a description of the habitat in Arizona.

Crotalus pricei miquihuanus. Although much literature is available about *C. p. pricei,* little is known about *C. p. miquihuanus* (Figs. 24, 25), no doubt due to the inability of collectors to get into the limited areas inhabited by it. Specimens of this rattlesnake have been known since 1898 when Nelson and Goldman succeeded

in capturing an adult male near Miquihuana, Taumaulipas. However, it was not placed as a subspecies of *C. pricei* until the holotype, a subadult male, was secured near Galeana, Nuevo León, in 1938, and described by Gloyd (1940: 102). Since that time, occasional specimens have been found but were unfortunately lost before being placed in systematic collections.

Recent information, still quite limited, presents a somewhat clearer picture of the apparent range of *C. p. miquihuanus.* In 1961 an adult snake of this race was collected in the Sierra de Los Amargos, Coahuila, extending the known range some thirty miles north from the type locality in Nuevo León (Axtell and Sabath 1963). This will probably become the range limit of this rattlesnake to the north, since there is a distinct topographical and faunal break at this site wherein a much more arid and desert-type habitat replaces the pine-oak forest of the Sierra Madre Oriental. J. R. Dixon (pers. comm.) secured three specimens of this race from 14.8-17.2 km E San Antonio de las Alazanas between 1981-2804 m elevation during May and August 1972. All were taken from a piñon-pine, agave slope. South from Cerro Potosí, the specimen obtained by Nelson and Goldman in 1898 is the only known record for this subspecies. This is not to suggest, however, that the area surrounding Miquihuana, Tamaulipas, is the southernmost limit of the range of *C. p. miquihuanus.* Due to topographical, faunal, and to some degree, geological similarity, it is possible that this sub-

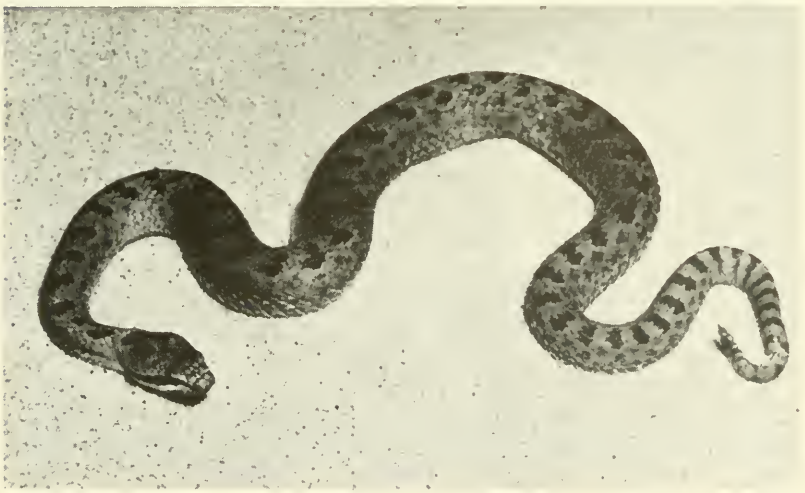

Fig. 24. *Crotalus pricei miquihuanus.* Specimen from near San Antonio de las Alazanas, Coahuila, Mexico. (Photograph by John H. Tashjian.)

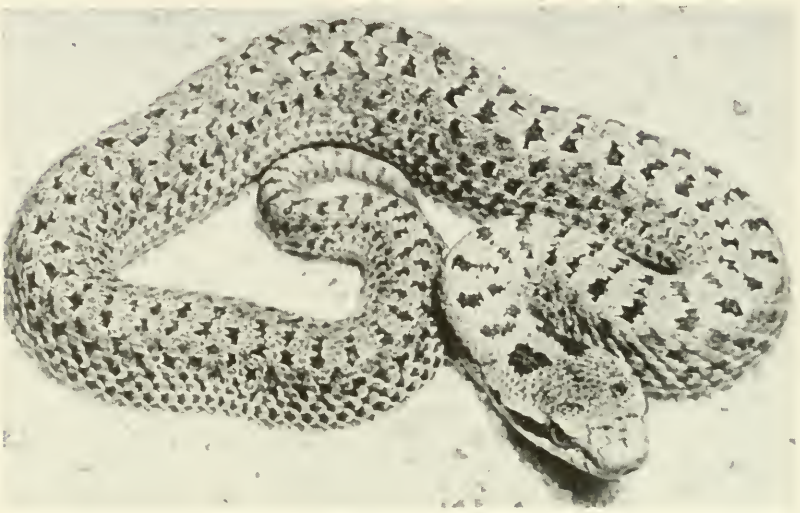

FIG. 25. *Crotalus pricei miquihuanus.* Juvenile specimen born to female collected from Cerro Potosí, Nuevo León, Mexico. (Photograph by John H. Tashjian.)

species will eventually be found as far south as the San Luis Potosí/southwestern Tamaulipas border, among the high forested mountain slopes.

During our travels throughout Mexico from 1967 to 1974, we secured four adult *C. p. miquihuanus.* Two were discovered above 3050 m near the type locality, in mid-July 1974, in a limestone bedrock, agave, scrub oak habitat at 1100 hours. They were both sunning on the limestone rock and seemed placid and indifferent to being captured, unlike *C. p. pricei* which reacts defensively. The summit of Cerro Potosí has been heavily deforested, and a luxuriant growth of low-growing vegetation, such as agave and scrub oak, has replaced the original pine forest. There are still many pines in the area, but Cerro Potosí is no longer strictly a pine forest. With this change in vegetation, the population of *C. p. miquihuanus* appears to have increased; possibly the low-growing shrubbery offers more protection to both the rattlesnake and its main food prey, lizards of the genus *Sceloporus.*

A female *C. p. miquihuanus,* collected on the east slope of Cerro Potosí, Nuevo León, at 3203 m, gave birth to five young (KU 155542, 157869-871) on 19 August 1974. The range of variation is as follows: total length 130-143 mm, mean 135; S-V 117-130 mm, mean 121; weight 2.6 g, mean 2.6. Another female (UTA R-6235) captured on 16 July 1976 in a pine-oak forest at 2652 m,

located 17.2 km E San Antonio de las Alazanas, gave birth to four young the following day (UTA R-6175-77, 6236).

The habitat type preferred by *C. p. miquihuanus* is the Temperate Pine-Oak association (Klauber 1956).

Crotalus pusillus Klauber

Crotalus pusillus is a small rattlesnake found in intermittent montane habitats in southern Jalisco and westcentral Michoacán (Figs. 26, 27). Klauber (1972: 163) considered this taxa to be one of the most primitive Mexican mountain rattlesnakes. *Crotalus pusillus* inhabits the pine-oak forests at elevations from 1525 m to at least 2380 m (Sierra de Coalcomán), and resides within the Upper Sonoran-Transition Zone as defined by Goldman (1951). It occurs sympatrically with *C. t. triseriatus* throughout its range with the exception of the Sierra de Coalcomán where possibly only *C. durissus culminatus* and *C. b. basiliscus* live in close proximity.

Crotalus pusillus is locally common, and 17 specimens were observed by us (UTA R-4530-1, 5846, 6119). We found them to be quite abundant in the Sierra de Coalcomán, in cleared areas of humid pine-oak forest (Fig. 28). Some specimens were taken in the early morning, but this animal was more easily located around 1200 hours, after the sun had burned off the low morning clouds. Duellman (1961: 658) suggested that this species was partially nocturnal. Several snakes were secured in cultivated fields where corn was planted between rock outcroppings. Others were located on and under fallen logs, and some were found in a rocky, grassy, agave situation. J. R. Dixon (pers. comm.) secured specimens from 14.4 and 20.9 km W Atenquique, Jalisco, under fallen bark in an oak forest between 1829-2164 m elevation.

Crotalus pusillus exhibits a typical behavioral pattern of rattlesnakes from high, humid, mountain areas. It will often reveal itself by rattling furiously when approached, but is comparatively less nervous than *C. lepidus* in similar encounters. Many of our specimens defended themselves vigorously upon discovery, and often would bite themselves or the tongs which were used to capture them. Ritualized combat between captive males has been observed by us. The stomach of an adult (UTA R-4530) contained an orthopteran.

A female collected near Dos Aguas, Michoacán, gave birth to one live and four stillborn young (KU 155545-548), and one infertile egg on 23 January 1974. Range of variation is as follows: total length 165-179 mm, mean 171; S-V 150-162 mm, mean 153; weight 3.0-6.1 g, mean 4.0. The surviving juvenile was maintained in cap-

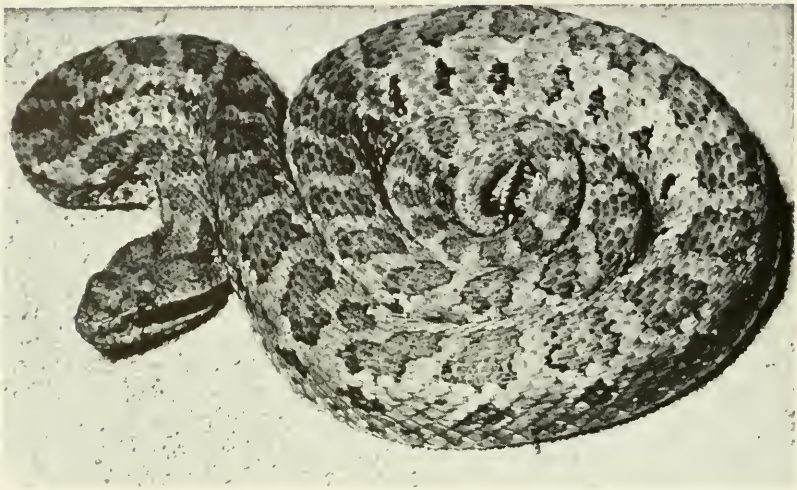

FIG. 26. *Crotalus pusillus.* Specimen from near Dos Aguas, Sierra de Coalcomán, Michoacán, Mexico. (Photograph by John H. Tashjian.)

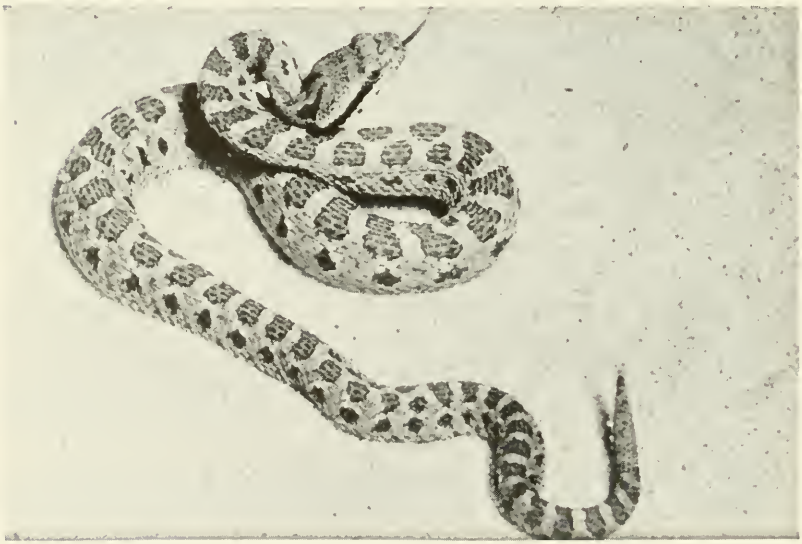

FIG. 27. *Crotalus pusillus.* Juvenile specimen from near Dos Aguas, Sierra de Coalcomán, Michoacán, Mexico. (Photograph by John H. Tashjian.)

FIG. 28. Habitat of *Crotalus pusillus* near Dos Aguas, Sierra de Coalcomán, Michoacán, Mexico, July 1974. Extensive limestone outcropping bordered by pine-oak forest. Snakes appeared more abundant in areas previously cleared for cultivation. (Photograph by Jonathan A. Campbell.)

tivity and bred, and gave birth to three young on 15 July 1976. Two of the young were stillborn within a single fetal membrane, and the mean weight and measurements for both are as follows: total length 111 m, S-V 98 mm, weight 1.1 g. The third neonate was alive at birth, measured 179 mm total length (156 mm S-V) and weighed 6.0 g (UTA R-7164).

On 24 March 1975 a pair of captive *C. pusillus* was placed together and a complete mating sequence was observed.

1130h Male placed in cage with female. Female had previously shed and defecated. Female immediately began twitching.

1130-1159 Male began spasmodic forward jerking (2 per sec) and tongue-flicking (2 per sec). Male loosely draped his coils over dorsum of female, bent head laterally at 90° angle to longitudinal axis of his body and, by contracting vigorously, pulled his head approximately 2.5 cm posteriorly along body of female. This action was performed repeatedly. Female raised tail 11 cm vertically and opened cloaca. Male became excited and investigated female's cloacal region. This entire sequence was repeated 34 times. Female twitched only occasionally.

1200 Male wrapped tail around female's head.

1201 Male released female's head and brought his cloaca to vent of female. Mating was not accomplished.

1202-1220 Both snakes remained quiescent.

1221 Female moved head, male lost grip and became excited.

1222-1400 Same pattern as above.

1401 Male and female simultaneously raised tails vertically, tightly wrapped tails, held position for 1 minute, then released.
1410 Female raised tail vertically (11 cm) for 5 minutes. Male continued to investigate.
1412 Both male and female raised tail 11 cm with cloacae juxtaposed giving appearance of a lyre. Distance between rattle matrix of both snakes was 6 cm. Male released position, then slid tail approximately 2 cm to cloaca of female. Male's tail was encircled around base of female's tail. Male slid tail rapidly and repeatedly along longitudinal axis of female's tail.
1417 Male's tail encircled base of female's tail twice.
1419 Male lost grip with his tail.
1424 Female raised tail.
1431 Female continued to raise tail, male inserted right hemipenis. A noticeable bulge was apparent eight ventral scale rows anterior to female's cloaca. Male continued to push against resistance of female which caused the female's tail to bend backwards over her body until the matrix of her tail was 3.5 cm above her vertebral column.
1443 Four quick pulsations at cloacal area of male.
1446 Male began undulations (2 per sec) which were within a vertical plane and were 5 cm anterior to the vent. During this period, the male constantly pushed the female's tail backward.
1500 Male tapped mental area of his lower jaw in a vertical plane on dorsum of female 39 times in a 6 minute period. No tongue flicks accompanied this behavior unless the male shifted position.
1509 Male tapped his lower jaw on dorsum of female 17 times, no tongue flicks.
1534 Pair still joined, diameter of female's cloaca was 12.5 mm which was distended due to male's hemipenis.
1740 Approximately 6 mm of base of hemipenis visible.
1800 Male pushed tail against female's tail, writhed for 3 seconds.
1834 Same as above.
1841 Both tails moved slowly for 10 sec.
1909 Observations discontinued.

The next day at 0800 hours the snakes had separated.

On 22 April 1975 the same male specimen was placed with a different female. The same behavioral patterns were observed, including upraised tails, bending of the female's tail backwards over her body, and pulsations. The head tapping behavior of the male was also observed. The raised tail of the female stimulated the male noticeably.

The habitat preferred by *C. pusillus* is mixed pine-oak forest and volcanic rock (Klauber 1956) and Pine-Oak Forest at an altitude of 1550 to 2300 m (Duellman 1965).

Crotalus ruber Cope

The red diamond rattlesnakes, *C. ruber*, of extreme southwestern California and adjacent Baja California, are among the largest and generally the most placid rattlesnakes we have observed. Partly because of their range and habitat preference, these snakes have been collected by one of us (BLA) every month of the year. Their peak period of activity is in late spring, and they are relatively

common throughout their range. In southern California, the status of *C. r. ruber* populations is becoming precarious as more and more developments claim inland valley habitats.

Crotalus ruber ruber. The northern subspecies, *C. r. ruber,* ranges from southeastern Los Angeles and Orange, San Diego, western San Bernardino, and Riverside counties, and extreme southwestern Imperial County in southern California, south to Loreto, Baja California del Sur where it intergrades with *C. r. lucasensis* (Klauber 1949a: 46). Klauber (1972: 46) also reported individuals from Monserrate, San Marcos, Pond, Ángel de la Guarda, and South San Lorenzo islands in the Gulf of California. It seems reasonable to assume that this rattlesnake will eventually be found on other, smaller islands that have not yet been thoroughly explored. It is interesting to note that a series of *C. ruber,* now known as *C. r. lorenzoensis,* from South San Lorenzo Island in the University of Colorado collection, show tendencies toward rattle loss (Radcliffe and Maslin 1975). This condition was seen on approximately 50 percent of the specimens. *C. r. ruber* obtained by us have been observed from various locations in five counties in southern California, and the following localities in Baja California: 6.4 km S Tijuana, the vicinity of Ensenada, the Hamilton Ranch (20 specimens) near Colonet, San Quintín, El Socorro (5 specimens), El Rosario, 16 km N Laguna Chapala, San Ignacio, 17.6 km W Santa Rosalia, 22.5 km S Mulegé. *Crotalus r. ruber* appears to be absent from the desert east of the Sierra de Juarez in Baja California del Norte.

In southern California, *C. r. ruber* is a resident of the hot inland valleys which include the Borrego Desert of San Diego County. It is found generally in areas of granite rock outcroppings, especially during winter months. During these months we have had success locating numbers of these snakes in the hottest part of the day. They are often coiled at the entrance of a gopher burrow, or in the midst of the rubble of a dilapidated barn. Rarely are they located any distance from some type of shelter. This rattlesnake is extremely lethargic during winter months, and defensive behavior is seldom observed even when it is provoked. However, during the late spring and summer months, *C. r. ruber* becomes increasingly nocturnal, and invades the grasslands between rock outcrops where it probably feeds to a large extent on cottontail rabbits, *Sylvilagus audubonii sanctidiegi,* and ground squirrels, *Citellus b. beecheyi,* both of which are abundant. In the true desert regions of its range, this snake is found near rocks, and seldom wanders from protective retreats. In the early spring, pairs of red diamond rattlesnakes are often observed basking together in full sunlight. Mating was observed in early April between a large pair in Railroad Canyon, just east of Lake Elsinore, California. The snakes were not collected.

Wagner (1964) characterized the vegetational characteristics of the area inhabited by *C. r. ruber* as California Chaparral, Seasonal Formation Series, and Cactus Scrub.

Crotalus ruber lucasensis. The southern subspecies of the red diamond rattlesnake, *C. r. lucasensis*, has a geographic range from the fishing village of Loreto to the Cape region of Baja California del Sur. Klauber (1972: 46) reported specimens of this race from Santa Margarita and San José islands. As with *C. r. ruber, C. r. lucasensis* may someday be found on other islands when they are thoroughly explored. Specimens obtained by us from the mainland were collected at El Triunfo, 8 km N San José del Cabo, and Buena Vista (B. Tomberlin, pers. comm.).

Barney Tomberlin (pers. comm.) reported that *C. r. lucasensis* was the most common snake in the Cape region of Baja California. Most of his snakes were taken in September when that area received a major portion of its annual rainfall. At that time they were nocturnal generally, and specimens were easily found by night driving. Although this rattlesnake can be found in the desert and open arid plains of southern Baja California del Sur, it is most common in heavy brush where rocks and rocky outcrops are prevalent.

This subspecies inhabits the Seasonal Formation Series and Cactus Scrub as defined by Wagner (1964).

Crotalus scutulatus (Kennicott)

Crotalus scutulatus was once confused with many of the other prairie dwelling rattlesnakes (Klauber 1972: 541), and therefore, much that has been written about it may, in part, be erroneous. It is a rather large, heavy-bodied snake that has a range similar to that of *C. molossus. Crotalus scutulatus* does not, however, inhabit the multiple habitats within its range as does *C. molossus. C. scutulatus* is found from the Mojave Desert and adjacent Nevada, south through Arizona, southwestern New Mexico, and Texas, and thence south into the Mexican central plateau.

Crotalus scutulatus scutulatus. *Crotalus s. scutulatus* is a common rattlesnake within its range in the United States. Klauber (1972: 47, 541) gave an excellent summary of the localities and field data for this race. In Mexico, we have found *C. s. scutulatus* throughout the flat, arid central plateau, but nowhere did it seem particularly common. Snakes captured and observed by us (approx. 30) were recorded from: CHIHUAHUA: the valley between the Sierra del Nido and Sierra de Santa Clara at 1982 m (UTA R-4554); SONORA: 12.8 and 17.6 km S Agua Prieta; DURANGO: La Zarca, 12.8 km N Rodeo, San Juan del Río; NUEVO LEÓN: Santa Fe (UTA R-4595), 12.8 km S Galeana, 8 km E San Roberto Junction; COAHUILA: 3.2 km W San Antonio; SAN LUIS POTOSÍ:

Matehuala, 4.8 km E Matehuala; ZACATECAS: 13.3 km E Junction of Mexican Hwy. 45 and 49 (UTA R-2715).

Miller and Stebbins (1964) noted that throughout the northern portion of its range, *C. s. scutulatus* appeared to be extremely nocturnal in behavior. Most of the specimens obtained by us were a result of night driving. In spring, it was not uncommon to find a specimen coiled at the base of a palo verde or creosote bush in early morning. During summer months, however, these snakes were rarely encountered during daylight hours. *Crotalus s. scutulatus* seems to prefer the open mesquite-creosote-cacti habitat within its range. It usually avoids true sand desert where *Crotalus cerastes* is the dominant rattlesnake.

In southern Arizona and adjacent Mexico, *C. s. scutulatus* is very common in prairie valleys (1220-1525 m) between the numerous forested mountain ranges of that region. Southward within the Mexican plateau this snake becomes crepuscular due to the higher elevations of the open, arid habitat. One individual obtained by us from grassland, juniper plain (1982 m elevation) near Santa Clara, Chihuahua, was located crossing a dirt road at 1100 hours in early July. In central Durango near the town of La Zarca, *C. s. scutulatus* was often seen in mid-afternoon crossing the highway or basking at the edge of the pavement. This area is approximately 2440 m elevation, and the daytime temperature is somewhat cool. Juniper and grassland are the dominant vegetation in this wind-swept region. Individuals from the eastern part of San Luis Potosí, especially around Matehuala, 1372 m, were also crepuscular in activity despite a lower elevation than at the Durango localities. Reese (1971) found *C. s. scutulatus* at a locality 77.2 km S San Roberto Junction in Nuevo León, and Banta (1962) found it at Cañada Honda, Aguascalientes. One adult snake obtained by us (UTA R-4554) contained rodent hair.

The Temperate Mesquite-Grassland and Desert as defined by Leopold (1950) are typical environments for *C. s. scutulatus.* See Gloyd (1937) and Lowe (1964) for a description of the habitat in Arizona.

Crotalus scutulatus salvini. *Crotalus s. salvini* (Fig. 29) is also a resident of open, high interior plains. It is found in Tlaxcala, Puebla, and west-central Veracruz, and its range is doubtless decreasing as these plains are cleared for cultivation. The type locality for this race, Huamantla, Tlaxcala (Klauber 1972: 147), at an elevation of over 2440 m, may now possibly be devoid of enough suitable habitat to sustain a population of these rattlesnakes. All of our specimens were collected within the lava beds near Perote, Veracruz, and Tehuacán, Puebla (Fig. 30). Both localities support luxuriant desert plant growth such as yucca, palmettos, and the giant, slender *Neobuxbaumia,* which are the most common plants.

Within the relatively undisturbed areas of its limited range, *C. s. salvini* remains a rather common snake, and, unlike *C. s. scutulatus,* is found in association with rocks. The lava beds of Perote seem to provide this rattlesnake excellent habitat. It may, however, be common there only because of man's encroachment upon the rolling, open, rockless plains where *C. s. salvini* was once, no doubt, the dominant member of the genus. Specimens of *C. s. salvini* obtained by us were all located during mid-afternoon in July and August, and were basking near porous volcanic rocks.

This rattlesnake is one of the most aggressive species we have encountered. Several struck so violently that their entire body appeared to be momentarily air borne. It is common behavior for them to strike even after being constrained in cloth bags for several weeks. *C. s. salvini* inhabits the Temperate Pine-Oak and Mesquite-Grassland vegetational areas as defined by Leopold (1950).

Crotalus stejnegeri Dunn

Crotalus stejnegeri is a primitive rattlesnake found in the mountains of southeastern Sinaloa and southwestern Durango. Klauber (1972: 542) reported two specimens that ". . . were found on the border of a pine forest, at the upper edge of a canyon dissecting a plateau." McDiarmid *et al.* (1976) reported an individual found on a road which was 3.3 km west of a pine forest, probably in subtropical dry forest (Hardy and McDiarmid 1969). Road temperature was about 27°C and air temperature *ca.* 24°C where the snake was collected. A small male (UTA R-5926) and female were collected at Plomosas, Sinaloa, at 1067 m on 3 August and 27 August 1976, respectively. The snakes were found in a transition area between pine-oak and tropical deciduous forest (Fig. 4). Vegetation in this area includes silk-cotton trees, morning glory trees, *Enterolobium, Coccoloba,* nanche *(Byrsonima crassifolia),* cassias, acacias, and mimosas (Goldman 1951). The male was found in a rock slide at the base of a bluff, and the female was secured in a small rodent burrow in a semi-open field. A large male (UTA R-6234; Fig. 31) was found on 15 August at Ejido Tebaira, Sinaloa, at 1067 m in a tropical deciduous forest. This individual measured 638 mm total length, 86 mm tail length, and is larger than the largest snake reported by McDiarmid *et al.* (1976).

Crotalus tigris Kennicott

Crotalus tigris is a medium to small-sized desert dwelling rattlesnake with a proportionately small head and large rattle. This species has a rather limited range, and is known only from the states of Arizona and Sonora. Wright and Wright (1957: 1001) considered this species rare.

Crotalus tigris is a resident of rocky foothills within the Sonoran

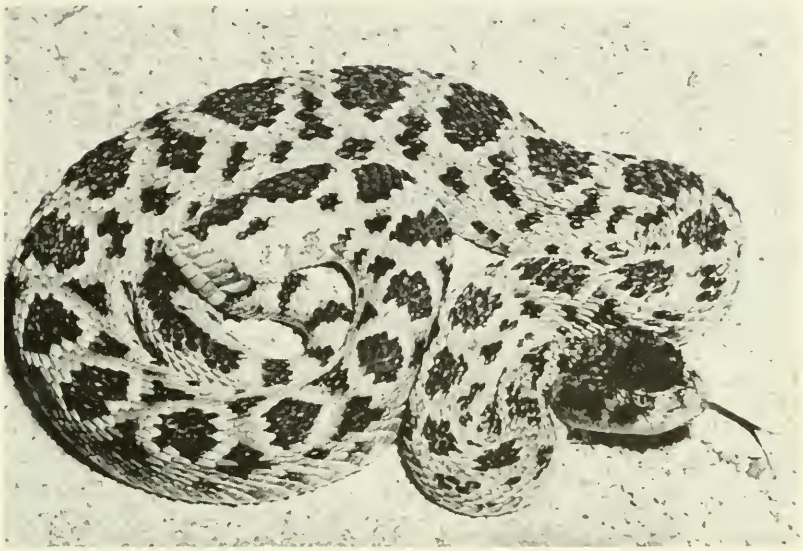

FIG. 29. *Crotalus scutulatus salvini.* Specimen from 1.6 km E El Limon Totalco, Veracruz, Mexico. (Photograph by John H. Tashjian.)

FIG. 30. Habitat of *Crotalus scutulatus salvini* and *Sistrurus ravus,* near El Limon Totalco, Veracruz, Mexico. Area is lava flow characterized by cactus, agave and grasses. (Photograph by R. Terry Basey.)

FIG. 31. *Crotalus stejnegeri.* Specimen from Ejido Tebaira, Sinaloa, Mexico. (Photograph by Jonathan A. Campbell.)

Desert of Mexico and the United States, and ranges from near sea level at La Posa, Sonora, to at least 1465 m elevation (Humphrey 1936). We found an individual snake at the same elevation on the western slopes of the Santa Rita Mountains, Arizona. Van Denburgh (1922) recorded the maximum elevation for this species at 2440 m. *C. tigris* is rarely found far from rocky retreats. Lowe (1964: 173) considered this rattlesnake to be strictly a rock dweller in rocky canyons, and on the hillsides and bajadas of desert ranges. Three snakes obtained by us from 11.2 km NE Scottsdale, Arizona (UTA R-6943, KU 155525) were taken at night in early July just after a thunderstorm. They were active among granite outcrops where cacti, palo verde, and creosote were abundant. This snake is nocturnal and rarely ventures forth before summer rains begin. Taylor (1936: 49) found two *C. tigris* at night, south of Hermosillo, Sonora, coiled in isolated rock outcrops in low mountains. We observed a snake of this species from the Tucson Mountains, Arizona, at night, as it was investigating a pack rat nest. This area is very rocky, with much desert vegetation. Dixon *et al.* (1962: 99) described the habitat of *C. tigris* in southern Sonora as scrub desert.

Crotalus tigris is behaviorally unpredictable. Two specimens from near Scottsdale were located when they rattled as we passed within 3 m of them. This observation occurred on an extremely warm, humid evening, after a thunderstorm. A specimen from the Tucson Mountains never rattled, even while being captured.

Klauber (1972: 453) felt that this rattlesnake was generally inoffensive, and not prone to rattle or strike.

The Seasonal Formation Series and Cactus Scrub as defined by Wagner (1964) are typical environments inhabited by *C. tigris*.

Crotalus tortugensis Van Denburgh and Slevin

Klauber (1972) characterized Tortuga Island off Baja California as rocky and barren, more arid than the mainland, with sparse brush and cacti. Three specimens of *C. tortugensis* obtained by us (KU 174832) were collected on 27 October 1975 in an area of lava boulders (D. Brown, pers. comm.). Wagner (1964) characterized the vegetational character of Tortuga Island as Seasonal Formation Series.

Crotalus transversus Taylor

Crotalus transversus is, biologically, a poorly known rattlesnake both in the field and in captivity. Its type locality was listed by Smith and Taylor (1950) as Tres Cumbres, Morelos, but Davis and Smith (1953) reassigned the type locality to nearby Laguna Zempoala, Mexico. The late E. H. Taylor (pers. comm.) informed us that the type locality is Tres Cumbres. Further collecting may reveal the presence of *C. transversus* in northwestern Morelos and southwestern Distrito Federal due to the topographical similarity of these regions to that of the type locality.

Only three individuals of this species have been recorded from the time of its discovery in 1942 until 1971. Since then nine specimens of *C. transversus* have been secured, six of which are discussed here (Figs. 32, 33).

On a trip to southern Mexico in the summer of 1973, Charles Radcliffe and one of us (BLA) succeeded in collecting five of these snakes (UCM 51421-3, KU 159361-2). An additional specimen was collected in May 1975 (UTA R-3988). All were taken at Laguna Zempoala, Mexico (Fig. 34) between 1 August and 5 August at elevations ranging from 2896 to 3293 m. The habitat was temperate boreal forest as defined by Leopold (1950). Five specimens were observed basking on south-facing slopes on volcanic rocks in the early afternoon. None of the specimens was basking in direct sunlight. The snakes were found after morning rain-showers which occur almost daily at this locality during summer months. Air temperature at the time of collection was between 16-20°C.

C. transversus is a very inoffensive rattlesnake, and retreats rather quickly when discovered. None of the captive specimens maintained by us rattled or struck, unlike *C. t. triseriatus* with which this species is sympatric. T. Walker (pers. comm.) observed that only one of his three captive specimens ever rattled, and believes that this species is not rare, but is only thought to be so

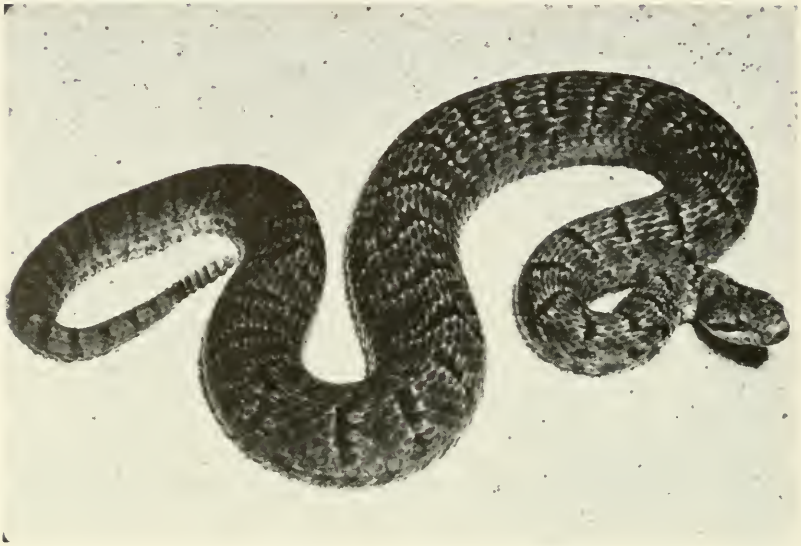

FIG. 32. *Crotalus transversus.* Specimen from near Laguna Zempoala, Mexico, Mexico. Reddish color phase with distinct cross-bands. (Photograph by John H. Tashjian.)

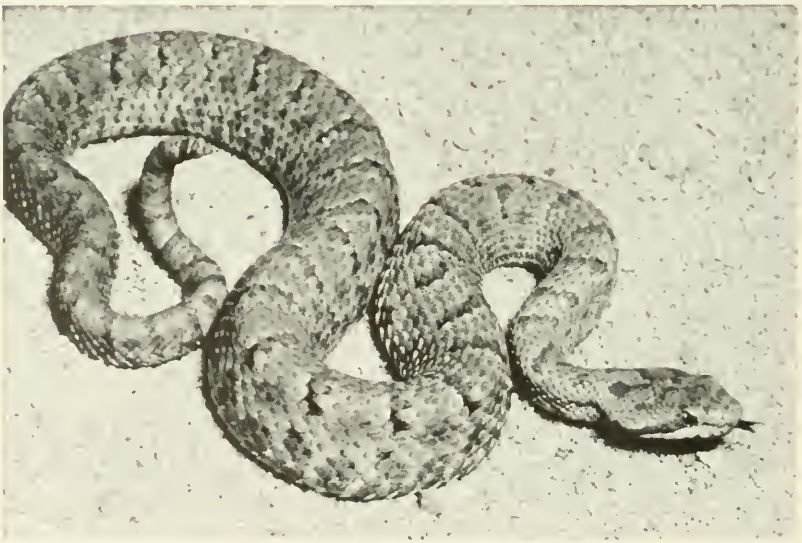

FIG. 33. *Crotalus transversus.* Specimen from near Laguna Zempoala, Mexico, Mexico. Grayish color phase with indistinct cross-bands. (Photograph by John H. Tashjian.)

FIG. 34. Habitat of *Crotalus transversus* and *C. triseriatus triseriatus* near Laguna Zempoala, Mexico, Mexico. Open fir-pine-oak forest with understory of bunchgrass. (Photograph by M. Granger.)

because of its limited activity periods in its natural habitat. An abundance of lizards and mice in the preferred habitat of *C. transversus* probably results in the need for only limited foraging activity. Klauber (1972) mentioned that one individual contained lizard scales, and one of our snakes defecated lizard scales, probably *Sceloporus aeneus.*

A number of food items were offered to captive *C. transversus:* treefrogs *(Hyla),* lizards *(Sceloporus, Gerrhonotus, Uta, Phyllodactylus, Xantusia, Cnemidophorus, Anolis),* wild rodents *(Mus musculus),* snakes *(Thamnophis, Nerodia),* newborn laboratory rats, sparrows, and domestic gray crickets *(Gryllus);* all were refused. The rodents were killed by the snakes, but the other potential prey items were ignored.

Captive snakes of this species were maintained by us at the following thermal levels: (1) 26.5°C during the day and dropping to 10°C at night; (2) 25-27°C during the day, 20°C at night; (3) low 20°C temperature at all times. These snakes may have been affected by the change in elevation from their native habitat to captive conditions. They fared badly at all three thermal levels.

Crotalus triseriatus (Wagler)

The dusky rattlesnakes of south-central Mexico are, taxonomically, one of the most complicated groups of rattlesnakes yet described. We have made over 100 observations of both subspecies, and this field work has shed some light on their relationships. It has become apparent to us that the two currently recognized subspecies, *C. t. triseriatus* and *C. t. aquilus,* require a complete review, and such work is underway by several of our colleagues.

Crotalus triseriatus triseriatus. *Crotalus t. triseriatus* is a montane race reaching the highest altitude (4572 m on Mt. Orizaba, Veracruz) at which any member of the genus *Crotalus* has been recorded (Klauber 1972: 516, 542). Although found at such high altitudes, *C. t. triseriatus* is more commonly encountered at elevations between 2743 m and 3353 m. Specimens have been recorded by us from: JALISCO: the mountain valleys N Nevado de Colima (UTA R-4909) (see Campbell, 1979); MEXICO: Laguna Zempoala; DISTRITO FEDERAL: La Cima; MORELOS: Tres Cumbres, the lava beds N Cuernavaca, Huitzilac (Fig. 35).

Crotalus t. triseriatus probably occurs in the Mexican state of Puebla, but we have no records as yet from that area. It also may be found on Cerro La Malinche, a 4267 m peak in Tlaxcala. Residents in this area described to us a snake which appeared to be *C. t. triseriatus,* but no specimens have been secured. In general, the range of *C. t. triseriatus* follows a narrow east-west belt between the 18th and 20th parallels. This range includes Cordillera Volcánica of southern Mexico.

Crotalus t. triseriatus is one of the most common forms of the small Mexican montane rattlesnakes. Due to the high elevations at which it occurs, this subspecies is almost entirely diurnal in activity. Even during the warmer months of the year, temperatures fall to levels at night which would not permit activity by this snake. Consequently, this rattlesnake is most easily observed in mornings and afternoons when the sun has sufficiently warmed its habitat. These animals are also active during the rainy season, and it is not uncommon to find several following an afternoon shower, basking on rocks that are still warm from the earlier rays of the sun. Davis and Smith (1953: 141) found *C. t. triseriatus* common near Huitzilac, Morelos, along streams that were bordered by a luxuriant growth of bunch grass. Our observations agree with theirs; this snake is rarely found any distance from a rocky, grassy environment. We have obtained snakes on rock slides near Laguna Zempoala, Mexico, but they are not nearly so common there. Duellman (1965) mentioned this species as an inhabitant of the Pine-Oak Forest at 1600-3270 m altitudes.

Crotalus t. triseriatus exhibits behavior that is comparable to that of other rattlesnakes in montane habitats. It is alert and ready to retreat when annoyed, yet curious enough to expose itself to capture. This subspecies is relatively unaggressive even when being captured. We have observed ritualized combat between captive males. *C. t. triseriatus* feeds on lizards and small rodents

FIG. 35. Habitat of *Crotalus triseriatus triseriatus* and *Sistrurus ravus*. La Cima, Distrito Federal, Mexico. Old lava flow covered with bunchgrass, formerly a pine forest. (Photograph by M. Granger.)

which are plentiful in its preferred habitat. Cursory examination of stools from freshly caught specimens supports this diet preference.

On 15 July 1970, a female from the northern drainage of Nevado de Colima, Jalisco, was located in a partially cleared pine-oak forest under a log, along with six new-born young. A captive female passed a partially formed embryo on 1 July 1976. Four young were born on 30 October 1975 to a captive female collected at Laguna Zempoala. Range of variation is as follows: total length 159-178 mm, mean 168; S-V 141-161 mm, mean 150; weight 4.8-5.1 g, mean 4.9. A captive pair was observed *in copulo* on 24 April 1975 at 0800 and were separated at 1400. The same pair also bred on 8 September 1977.

Crotalus triseriatus aquilus. The northern subspecies of this rattlesnake, *C. t. aquilus* (Figs. 36, 37), does not reach the high altitudes inhabited by *C. t. triseriatus.* It seems to prefer the open, grassy habitats north of the Cordillera Volcánica. Specimens assignable to this subspecies have been recorded by us from: MICHOACÁN: 16 km W Jiquilpan; SAN LUIS POTOSÍ: the vicinity of Alvarez; HIDALGO: Jacala, San Vicente, Durango, El Chico (KU 155549-553, 155556; UTA R-4540, 6941), La Estanzuela (UTA R-4675, 6115).

This rattlesnake is a common montane snake, but, as previously stated, does not usually occur in extremely high-altitude habitats. Klauber (1972: 517) gave 2438 m elevation, near Jacala, Hidalgo,

FIG. 36. *Crotalus triseriatus aquilus.* Juvenile specimen from near El Chico, Hidalgo, Mexico. (Photograph by John H. Tashjian.)

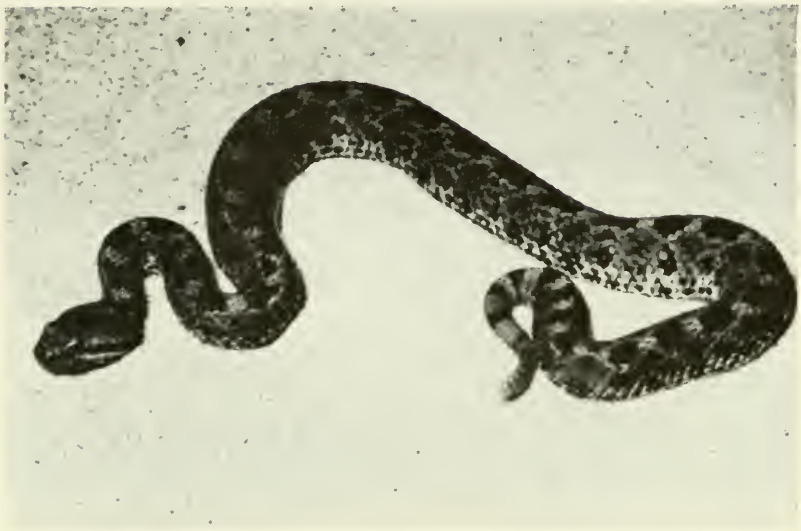

FIG. 37. *Crotalus triseriatus aquilus.* Specimen from near El Chico, Hidalgo, Mexico. (Photograph by John H. Tashjian.)

as the highest point where *C. t. aquilus* has been collected. However, we have located a population near El Chico, Hidalgo (Fig. 38) where these rattlesnakes have been found up to 3110 m in a fir forest. The snakes from this population, while falling well within the known geographic range of *C. t. aquilus,* are quite different from our other specimens of this race. They are larger and exhibit a greenish hue, with males far exceeding females in size and brightness of color. These specimens tend to be heavier bodied than typical *C. t. aquilus* and they are extremely alert and aggressive. In many characteristics they resemble *C. lepidus.* Further study of these specimens is needed in order to understand their status in relation to other populations of *C. t. aquilus.*

Generally, *C. t. aquilus* is an inhabitant of pine-oak forests and open mesquite-grasslands of the southern central Mexican plateau (Fig. 39). Snakes from Michoacán, the southernmost portion of the range of *C. t. aquilus,* usually inhabit mesquite-grassland. Northward to Hidalgo and San Luis Potosí, this race tends to occur more commonly in the pine-oak forests where there is an abundance of rock outcroppings.

The behavior of *C. t. aquilus* in the field is much the same as that of *C. t. triseriatus,* but individuals of the former tend to be somewhat more aggressive and easily agitated. These snakes often reveal their presence by rattling when alarmed, as is typical of

FIG. 38. Habitat of *Crotalus triseriatus aquilus*, near El Chico, Hidalgo, Mexico. Fir forests cover hills reaching elevations exceeding 3110 m. Snakes most commonly found in open rocky outcrops. (Photograph by Jonathan A. Campbell.)

FIG. 39. Habitat of *Crotalus triseriatus aquilus*, near San Vicente, Hidalgo, Mexico. Steep hillsides are covered with pine-oak forest. Snakes most common in open limestone bedrock. (Photograph by R. Terry Basey.)

C. lepidus. This race is active in the mornings and afternoons, but unlike *C. t. triseriatus,* it may be found foraging at night. We have found them while driving at night in the vicinity of Durango, Hidalgo, a somewhat humid area where night temperatures are occasionally favorable for activity. Ritualized combat between captive males has been observed by us.

Two females of *C. t. aquilus* from El Chico, Hidalgo, gave birth to six and seven young on 7 June 1974 and 29 July 1974, respectively. Range of variation of the two broods is as follows: total length 168-192 mm, mean 178; S-V 153-177 mm, mean 163; weight 5.0-8.8 g, mean 6.4. Another female, collected 16 km W Jiquilpan, Michoacán, gave birth to three young on 29 June 1974. Range of variation is as follows: total length 164-171 mm, mean 167; S-V 150-156 mm, mean 152; weight 5.0-6.4 g, mean 5.5. A captive pair of *C. t. aquilus* from El Chico was observed copulating on 28 April 1975. One of these snakes later gave birth to two viable and one deformed young on 27 July 1977, and the measurements and weights are as follows: total length 120-181 mm, mean 150; weight 4.9-7.8 g, mean 6.3. The deformed snake exhibited a fusion of the ventral surface in the lower cervical area (UTA R-6940). Another pair of *C. t. aquilus* was joined in mating at 0830 hours on 26 October 1977. The female's cloaca was distended and the male's body pulsated (twice per second) near the vent during coitus. The uplifted tails of the snakes produced a venter-to-venter configuration in the region of the cloaca. Separation occurred at 0901, and detumescence of the hemipenis occupied 7 seconds.

Duellman (1965) characterized the vegetational character of the habitat of this rattlesnake as Mesquite-Grassland and Pine-Oak Forest at 1600-2000 m altitudes. This race is found in the Temperate Mesquite-Grassland and Pine-Oak Forest as defined by Leopold (1950).

Crotalus viridis (Rafinesque)

Crotalus viridis caliginis. *Crotalus v. caliginis* is a race found on South Coronado Island off the northwest coast of Baja California. This area is rocky with brush and cacti, and two adult specimens (KU 174835, UTA R-6945) were collected at the north end of the island on 25-26 June 1976 (D. Brown, pers. comm.). The female passed one partially formed embryo on 14 August 1976.

This subspecies is found in the California Chaparral as defined by Wagner (1964).

Crotalus viridis helleri. *Crotalus v. helleri* is a subspecies found in southern California and northern Baja California, and is a resident of almost every habitat within its range. As with *C ruber,* with which it shares a great deal of its range, a number of *C. v. helleri* have been observed by us every month of the year. These

snakes vary greatly in color and pattern within a given population. As individuals of this rattlesnake age, they apparently lose their pattern or it fades greatly, a common trait of all races of *C. viridis*. Most larger specimens of *C. v. helleri* are black or very dark with little pattern. Many young of this race have distinctly patterned heads, but this fades at an age of two years on most individuals.

C. v. helleri ranges from San Luis Obispo and Kern counties south through southern California (avoiding only the true deserts in the eastern part of the state) and continues into Baja California as far south as Playa María Bay on the west coast, and near Bahía de Los Ángeles on the east coast (Klauber 1949b: 83). Murray (1955: 47) reported a specimen 32 km SE Mesquital, some 88 km south of Klauber's (1949b: 83) southernmost record. Smith *et al.* (1971) found two specimens 69 km WNW Bahía de Los Ángeles and 16 km S El Arco. Specimens from these southernmost locations are rare, although it is possible for *C. v. helleri* to inhabit the area as far south as San Ignacio in central Baja California. Rattlesnakes obtained by us come from many localities in southern California, but we have few records from Baja California. Individual specimens from Mexico have been observed from Punta Camalú, north of Ensenada, and the western slopes and interior peaks within the Sierra Juárez.

Crotalus v. helleri is common within its range, although its numbers seem to decrease in the southern portions. On the lower slopes of the San Gabriel Mountains in Los Angeles County, California, the populations of this race are as concentrated as any of the genus known to us. This is a rugged, rocky area with chaparral, and the rainy season occurs in the winter and early spring. Rattlesnakes have been found from the edges of the San Gabriel River to the hot, sparsely vegetated, south-facing slopes and pine-oak slopes facing the north. Although individuals of *C. v. helleri* in this area do not den or hibernate as such, they do congregate in rock slides or rock outcrops which face the south or east during rainy, winter months. To the south in Orange, Riverside, and San Diego counties, this subspecies is found from the Pacific coast in rolling, grassy savannahs to at least 3200 m in a pine-fir forest on Mt. San Jacinto. Throughout most of these southern California counties, *C. mitchelli pyrrhus* and *C. r. ruber* live sympatrically with *C. v. helleri*. We have observed all three rattlesnakes within 45 m of each other near Warner Hot Springs, just north of the Borrego Desert. In that particular area, all three species seem equally abundant. Elevation in this area is approximately 1068-1220 m. In 1967 one of us (BLA) found an apparent hybrid, *C. v. helleri* × *C. r. ruber*, on the road in this same general area. Reports of hybrids from this area are not uncommon.

In Baja California, *C. v. helleri* is much less common and is

apparently replaced by *C. enyo furvus, C. r. ruber,* and *C. mitchelli pyrrhus.* A snake from Camalú was observed in scrubby, coastal vegetation approximately 9 m from the shoreline. Another example from the western slopes of the Sierra Juárez was found basking in diffused sunlight under a manzanita bush. Klauber (1949b: 83) reported a specimen 16 km NW Bahía de Los Ángeles in desert mountains in an elephant tree association.

Crotalus v. helleri tends to be a rather aggressive form and is easily agitated, behavior reported by Klauber (1972: 454). Most adults will defend themselves vigorously.

Wagner (1964) characterized the vegetational character of the habitat of *C. v. helleri* as California Chaparral and Montane Formation Series, and Leopold (1950) characterized it as Pine-Oak Woodland and Piñon-Juniper Woodland.

Crotalus willardi Meek

The ridgenose rattlesnake, *C. willardi,* is an example of a small, montane species whose biology has remained somewhat obscure, no doubt due to difficulties encountered in reaching possible Mexican collection localities. Little is known of its habits, but it does not appear to be rare within its range. The four races of this species collectively inhabit the Sierra Madre Occidental from southeastern Arizona and southwestern New Mexico, southeasterly to southern Durango and western Zacatecas (Klauber 1949c: 125).

Crotalus willardi willardi. The northern subspecies, *C. w. willardi,* is a resident of the pine-oak forests of the Huachuca and Santa Rita Mountains in Arizona, and the Sierra de Ajos and Cerro Azul in Sonora, Mexico. This rattlesnake seems to prefer the more humid canyon bottoms of pine-oak habitats as opposed to exposed arid slopes where *C. lepidus* and *C. pricei* are common. B. Tomberlin and R. T. Basey (pers. comm.) reported that individuals from the Sierra de Ajos (UTA R-6689, R-6928-30) were common in the wide, rocky stream beds where pools of water remained after summer rains. This was between 1982 m and 2287 m in elevation. Two lizards (*Sceloporus jarrovi* and *S. undulatus*) were common in this stream bed habitat, and no doubt contribute a major portion to the diet of this snake. Klauber (1972: 642) mentioned a specimen that contained a brush mouse *(Peromyscus boyli).* Although preferring the cooler, humid canyons, *C. w. willardi* is in no way restricted to this habitat. A snake from upper Madera Canyon at 2593 m in the Santa Rita Mountains was observed on an east-facing slope amidst broken rock and scrub oak. It would have been overlooked had it not rattled, for the area where it was found is steep and the scrub oak nearly impenetrable. A specimen of *C. pricei* was located nearby. *C. w. willardi* is most active on warm, humid days when the sunlight is intermittent. It is especially common

before and after an afternoon shower when the temperature is between 24-29°C.

Crotalus w. willardi is typical of the small, montane rattlesnakes in that it is nervous and irritable, although not to the degree exhibited by *C. lepidus* or *C. pricei.* At times it reveals its presence by rattling, and will crawl to safety upon the least provocation. Captured specimens are more apt to turn and bite, as opposed to typical rattlesnake striking behavior. Kauffeld (1943b: 357) and Stebbins (1954: 484) also found this to be true. After a short period of time, captive specimens of *C. w. willardi* generally calm down and maintain a peaceful disposition.

Martin (1975a, 1975b) discussed reproduction in *C. w. willardi.* On 18 April 1971 a captive pair was observed by us *in copulo* at 0800 hours, and they were still joined at 1700 hours when observations were discontinued. There were no results from this mating.

Crotalus w. willardi is found in the Montane Formation Series and Montane Thicket as defined by Wagner (1964) and Pine-Oak Forest and Pine-Oak Woodland as defined by Leopold (1950). See Gloyd (1937) and Lowe (1964) for a description of the habitat in Arizona.

Crotalus willardi amabilis. Five adult (KU 178794; Fig. 40) and four subadult *C. w. amabilis* (UTA R-7162) were taken in Arroyo Mesteño, Sierra del Nido, Chihuahua, at 2440 m on 18, 19, 21 July 1977 (L. A. Mitchell and D. G. Barker, pers. comm.). Most of the snakes were located at the bases of small trees in piles of twigs and leaf litter near streams; one was found in a shin-oak association. The area had been logged three times in twelve years, and the last logging had occurred four years earlier. All snakes were visible, some coiled and others crawling, and only two rattled when captured. Intermittent thunderstorm activity had occurred for two weeks prior to 18 July, and occasional showers occurred during the collecting period. The ambient temperature was *ca.* 21°C, and the snakes were found throughout the day. Two *C. p. pricei,* one within 5 m of an *C. w. amabilis,* and two *C. lepidus klauberi,* one in scrub-oak and the other in a talus slope near shin-oak, were also found. Two *C. w. amabilis* defecated rodent hair in the laboratory. R. K. Guese (pers. comm.) observed a captive male courting a female on 8-9 September 1977. The female remained in a resting coil and the male directed head-bobbing and tongue-flicking across the female's dorsum (3-5/5 seconds). The male moved his uplifted tail in both a horizontal and vertical plane with an undulating motion. Physical contact with the side of the enclosure or the substrate stimulated this behavior which we interpret as Tail Search Copulatory Attempts. The sequence lasted 5 minutes.

Crotalus willardi meridionalis. The southernmost subspecies, *C. w. meridionalis,* inhabits a limited area in southern Durango and

extreme southwestern Zacatecas, and few specimens are available for study (Gloyd 1940; Klauber 1972). Like its sister races, *C. w. meridionalis* is a montane inhabitant rarely found below 2440 m. This subspecies is not generally a canyon-bottom dweller. The area inhabited by it is high (2440 m) pine-covered plateaus where open meadows provide breaks in the forest. Five individuals obtained by us from near Llano Grande, Durango (Fig. 23; UTA R-5639-41, 6124-25), were collected on 4 August 1975 on a partially open hillside which sloped into a grassy meadow. The slope had a northern to northeastern exposure. All specimens were located at *ca.* 2560 m at a temperature of 21-24°C between 0830 and 1000 hours. It had rained the previous evening and continued until 0600 when the sun appeared. The environment was humid when the rattlesnakes were captured, and none was found after the high clouds had disappeared. The habitat, although not a canyon, was similar to that occupied by other races of *C. willardi.* It was composed of sparse short-needled pines mixed with equally sparse oak and madroño. Rocks were scattered throughout the scrub-oak, and grassy ground cover provided excellent retreats. All five specimens were newborn young and had shed their skin at least once. They exhibited gentle dispositions and refused to bite upon capture. An adult male *C. w. meridionalis* was found on 18 July 1976 at the crest of a partially denuded hill with a low dense covering of scrubby brush. It was basking in direct sunlight at 1100 hours. An adult female, opaque-colored prior to shedding, was discovered at

FIG. 40. *Crotalus willardi amabilis.* Specimen from Arroyo Mesteño, Sierra del Nido, Chihuahua, Mexico. (Photograph by Jonathan A. Campbell.)

1000 hours on 12 July 1977 during an intermittent rainstorm. Heavy fog shrouded the area in the early morning. The ambient temperature was *ca.* 21°C, and the snake was resting in shade. Seven additional snakes (one preserved, KU 178975) were taken in the upper regions of the mountains at a ranch near the city of Durango (S. Prchal, pers. comm.).

This snake inhabits the Montane Formation Series as defined by Wagner (1964).

Crotalus willardi silus. *Crotalus w. silus* (Fig. 41) is also a resident of the temperate, pine-oak forests in the Animas Mountains of New Mexico (Bogert and Degenhardt 1961), the adjacent Sierra de San Luis, the Sierra de la Purica (Sierra de Nacozari) in Sonora, and the mountains to the immediate east and south of Chihuahua (Fig. 42). *Crotalus w. silus* is very similar to *C. w. willardi* in its habitat preference. Snakes from the Animas and San Luis ranges, however, exist in a much drier climate since these mountains receive less rainfall than mountains which support other *C. willardi* populations. Three individuals observed by us in the Animas Mountains were found in late October and early May when it was very dry. All three specimens were located at an elevation of 2120 m on east-facing slopes where pines, scrub oak, and manzanita comprised the major vegetation. None of the snakes rattled or tried to escape, unlike other *C. w. silus* from humid habitats.

We observed approximately 40 *C. w. silus* between 1970 and 1974 in the Sierra de la Purica in northern Sonora (KU 155554-555,

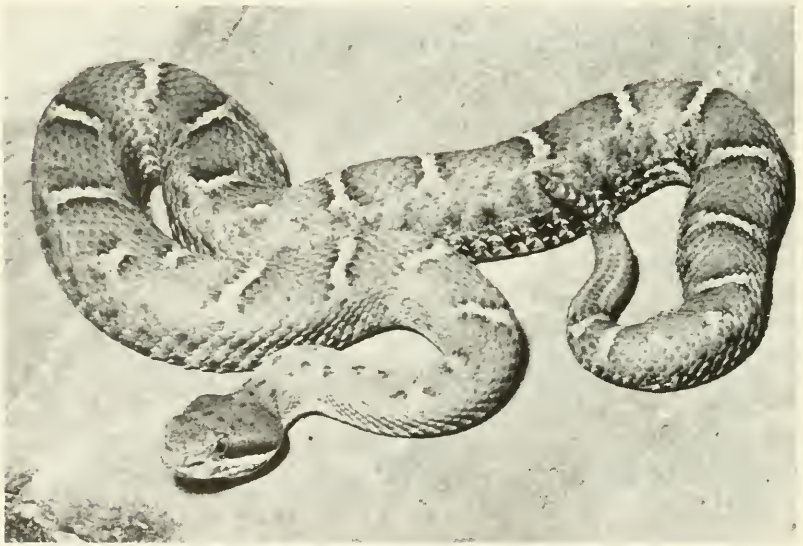

FIG. 41. *Crotalus willardi silus.* Specimen from Sierra de Nacozari, Sonora, Mexico. (Photograph by John H. Tashjian.)

158562, UTA R-6942). No other member of the genus has been observed in this range, which contains perfect *C. willardi* habitat consisting of long, large canyons with a south to north stream-flow where water is present throughout the year. Pines and oaks dominate the vegetation with sycamores in stands along the wide canyons. Ferns and poison oak provide ground cover in the rocky stream beds, where *C. w. silus* is most prevalent. Snakes have been seen from April through October, with the greatest numbers being observed in the July-August rainy season. At this time, generally cloudy skies and high humidity provide excellent conditions for these snakes. On one morning in early July we observed eleven specimens in a two hour period while hiking in a single canyon at elevations of 1630 m to 2300 m. Most of the snakes appeared to be foraging, since only one of the eleven was observed in a coiled, basking position. Of the four specimens collected that morning, one gravid female gave birth to five viable young on 7 August 1970. Another contained four fully developed embryos.

Ten females and one male were observed in the Sierra de la Purica between 15-23 July 1978. One pair was copulating on 15 July, and two adult females appeared as though they had just given birth. Another female gave birth to four young (KU 179025) on 10 August 1978. Total length of the four ranged from 146-218 mm, mean 190; S-V 129-193 mm, mean 168; weight 4.9-6.9 g, mean 6.0.

FIG. 42. Sierra de la Purica (Sierra de Nacozari), Sonora, Mexico. Habitat of *Crotalus willardi silus*. Canyon bottoms run south to north, pine-oak forest with ferns, poison oak, sycamore trees. Aspens in upper regions. (Photograph by R. Terry Basey.)

On 17 April 1971, captive breeding was observed. The female was placed with the male at 0800 hours. The male appeared to recognize the presence of the female within 10 seconds, began twitching (1 twitch per second), and tested the entire dorsal surface of female's body with his tongue (2 tongue-flicks per second). The male rubbed along the dorsal surface of the female for approximately 5 minutes by holding his head at 30° angle and sliding the area of the mental scale forward for 1 cm. Other mating dates recorded were 19 April 1971 and 29 January 1973. The matings were unsuccessful.

An interesting observation was made by us concerning the brown coloration of individuals of *C. w. silus* from the Sierra de la Purica. Those specimens collected or observed above the waterfalls (2070 m) tended to be light brown, resembling the dominant pine needle litter. Other specimens from below the waterfalls tended to be a much darker brown, resembling the more dominant oak leaf litter. Specimen size was apparently not a factor in this difference in color.

Sistrurus ravus (Cope)

Sistrurus ravus is a resident of the tableland of south-central Mexico. It occurs in a variety of habitats within that tableland, ranging from nearly 3050 m in pine-oak forest near Huitzilac, Morelos, to about 1525 m in agave-cacti habitat of the valleys which surround the city of Oaxaca in central Oaxaca. Specimens have been recorded by us from: PUEBLA: Zacapoaxtla, Cacaloapan, Puebla (J. A. Campbell, pers. comm.); TLAXCALA: near San Dionisio; DISTRITO FEDERAL: La Cima; MORELOS: Huitzilac, the lava beds north of Cuernavaca; OAXACA: near Mitla, Ixtlán de Juárez.

Within its known range, S. *ravus* is a very common rattlesnake. It seems to be rather gregarious, at least in mountain valley habitats. We have observed over 100 S. *ravus* under many varied conditions, and it appears to be a very adaptable species. For example, near Huitzilac, Morelos, a large forested area had been cleared, perhaps 30 years ago, and now consists of tall bunch grass (Fig. 43). *Sistrurus ravus* has occupied this area and has become so common that the local people are extremely aware of its presence. The population from this particular area (at an elevation of 2866 m) contains the largest examples of this snake of all the localities where we have collected them. Several males measured 76 cm and engaged in ritualized combat in captivity. Many of these males tend to be melanistic, a characteristic that Klauber (1952: 114) noted in these snakes from Tres Cumbres, Morelos.

Although S. *ravus* seems to prefer grassy mountain valleys, it

is not restricted to that habitat. It is common in the lava beds north of Cuernavaca, Morelos, where it is sympatric with *C. t. triseriatus* and *C. molossus nigrescens*. *S. ravus* from this area are much smaller than the Huitzilac specimens. In parts of Puebla, Veracruz, and adjacent Oaxaca, *S. ravus* is found at lower elevations in areas of grass, agaves, cacti, and small, stunted oaks (Fig. 30). Individuals in this habitat appear to be more dispersed and were encountered less frequently.

In the spring of 1974, Jonathan A. Campbell and one of us (BLA) located an unreported disjunct population of *Sistrurus* in the central highlands of Guerrero. This population is removed some 330 air kilometers from the range of *S. ravus* as plotted by Klauber (1956: 58; 1972: 64), and is isolated from other populations by the Rio Balsas basin to the north and the Chilpancingo gap to the east. A complete description of this Guerreran population is forthcoming (Campbell and Armstrong, 1979). However, we think it proper to describe here the habitat and habits of these snakes. They are residents of the pine-oak forests of the Sierra Madre del Sur, and all of our specimens were secured in large, brushy flood plains at various elevations between 2975-3105 m. The first snakes were secured in mid-May during the warmer parts of the day. This region receives *ca.* 1500 mm of rainfall from May through October (Page 1930). According to the local inhabitants, frost does not occur at these elevations in the Sierra Madre del Sur, a large mountain

FIG. 43. Huitzilac, Morelos, Mexico. Habitat of *Sistrurus ravus*. Snakes extremely abundant in bunchgrass meadows bordered by fir-pine-oak forest. (Photograph by M. Granger.)

range that is rugged and steep, and would seem to offer little suitable habitat for grassland dwellers such as rattlesnakes of the genus *Sistrurus*.

The habits of Guerreran S. *ravus* are comparable to those from the southern central plateau. They are alert and quick to retreat when encountered, but will stand their ground when escape is impossible. Like most *Sistrurus*, they are more apt to turn and bite rather than coil and strike. Stools of some specimens contained rodent hair.

A female of this species from the vicinity of Huitzilac, Morelos, gave birth to seven young on 1 June 1974. Two other females from the same locality gave birth on 28 May 1975 to nine and three young respectively. The range of variation of the three broods is as follows: total length 160-208 mm, mean 183; S-V 138-192 mm, mean 166; weight 3.9-7.4 g, mean 5.4. A captive pair from Huitzilac was observed *in copulo* on 1 May 1976.

This rattlesnake inhabits the Temperate Pine-Oak Forest as defined by Leopold (1950).

DISCUSSION

The following observations and discussion present our views on various aspects of the biology of Mexican rattlesnakes, and indicate areas where research is needed concerning the ecology and behavior of these animals.

Habitat. Most montane species from Mexico were closely associated with rocky areas and such microhabitats allowed maximum protection. *Crotalus l. lepidus, C. l. klauberi, C. p. pricei,* and *C. m. molossus* were often located in talus slopes. Other montane rattlesnakes were found in pine-oak forests, mesquite grasslands and highland deserts but usually rocky outcroppings were the dominant feature. *Crotalus transversus* occurred in areas of volcanic rock, whereas *C. pricei miquihuanus* was found in situations with limestone bedrock. Some of the lowland taxa such as *C. durissus culminatus* inhabited arid tropical scrub forest with rocky outcroppings. Rattlesnakes were rarely found in cloud forests.

When first discovered, smaller montane taxa such as *C. intermedius, C. lepidus, C. pricei, C. pusillus, C. transversus,* and *C. willardi* would often rattle and quickly crawl to safety within rocks. Many of these rattlesnake taxa seemed to utilize specific retreats, for in some cases the snakes crawled toward the collector in their endeavors to escape, when suitable retreats were available in the opposite direction.

Our field experience indicated that Mexican rattlesnakes from higher elevations were most often encountered in microhabitats with a southern exposure *(C. i. intermedius, C. lepidus klauberi, C. l. morulus, C. m. molossus, C. p. pricei, C. transversus).* A few

taxa that appeared to vary from this mode were more frequently found in microhabitats with southeastern *(C. lepidus maculosus, C. m. molossus, C. viridis helleri),* eastern *(C. pricei miquihuanus, C. w. willardi, C. w. silus),* northern and northeastern *(C. willardi meridionalis),* and western exposures *(C. intermedius gloydi).*

Nearly all montane rattlesnakes were found above a 1800 m contour. Lowland taxa which invade the Mexican highlands included *C. durissus, C. molossus,* and *C. basiliscus. Crotalus molossus* and *C. scutulatus* inhabited lower elevations in the northern part of the range. A narrow vertical distribution at relatively low elevation characterized the habitat of *C. stejnegeri* (and perhaps *C. lannomi*). *Sistrurus ravus* avoided steep hillsides, but was found on gentle slopes or in valleys. It was not necessarily associated with rocky outcroppings, and was found also in lava beds, bunch grass bordered by fir forests, pine-oak forests, and areas of grass, agave or cactus.

Degree of slope inclination delineated the habitat of some Mexican rattlesnakes. *Crotalus pricei, C. pusillus, C. intermedius, C. transversus* and *C. lepidus* often inhabited extremely steep slopes whereas *C. willardi* was found in mountain valleys, usually with permanent water. *Crotalus polystictus* and *Sistrurus ravus* preferred relatively flat areas.

Ground cover is evidently a significant characteristic in the habitat of some Mexican rattlesnake taxa, and varied from light *(C. polystictus)* to intermediate *(C. pusillus, C. triseriatus, S. ravus). Crotalus transversus* and *C. triseriatus* (in some areas) inhabited relatively open situations with a heavy canopy.

Daily activity. Daily emergence of Mexican rattlesnakes from retreats, particularly montane taxa, was associated with diffused sunlight and high atmospheric humidity. Immediately following thunderstorm activity, rattlesnakes began to emerge and were often encountered basking on rocks which were still moist. In general, highland forms tended to be diurnal and the lowland taxa, especially during summer months, were nocturnal. The following Mexican rattlesnake taxa were found abroad by day: *C. b. basiliscus, C. b. oaxacus, C. cerastes, C. durissus tzabcan, C. i. intermedius, C. i. gloydi, C. i. omiltemanus, C. l. lepidus, C. l. klauberi, C. l. maculosus, C. l. morulus, C. mitchelli muertensis, C. m. molossus, C. m. nigrescens, C. polystictus, C. p. pricei, C. p. miquihuanus, C. pusillus, C. r. ruber, C. s. scutulatus, C. s. salvini, C. stejnegeri, C. tortugensis, C. transversus, C. t. triseriatus, C. t. aquilus, C. viridis helleri, C. w. willardi, C. w. amabilis, C. w. meridionalis, C. w. silus,* and *Sistrurus ravus.* The following Mexican rattlesnake taxa were found as they were prowling by night: *C. atrox, C. cerastes, C. d. durissus, C. d. culminatus, C. d. totonacus, C. e. enyo, C. e. furvus, C. l. lepidus, C. m. mitchelli, C. m. pyrrhus, C. m.*

molossus, C. polystictus, C. pricei miquihuanus, C. r. ruber, C. r. lucasensis, C. s. scutulatus, C. tigris, and *C. triseriatus aquilus.*

Adult snakes of three taxa *(C. intermedius omiltemanus, C. l. lepidus, C. t. triseriatus)* remained in the same location for a period of over two weeks and utilized the same rock for basking daily. Juveniles of these taxa were encountered prowling by night, perhaps to avoid predation while dispersing.

During the rainy season, pairs of *C. intermedius omiltemanus* were encountered in the field.

Seasonal Occurrence. The onset of the rainy season in Mexico stimulates rattlesnake seasonal activity. For example, 55 specimens of *Crotalus polystictus* from southwestern Jalisco were observed during a three day period in the rainy season, whereas only three snakes were seen during a comparable period in May before the beginning of the rains. Seventeen specimens of *C. lepidus morulus* were found during one day after the first major rain near Galeana in the Sierra Madre Oriental; only three individuals were seen during June. The seasonal activity of most other Mexican rattlesnake taxa corresponded to the pattern noted above. Exceptions included *C. l. lepidus* and *C. l. klauberi* which were found throughout the year if the temperature was warm. These two taxa have adapted to a more arid environment.

Faunal and Climatic Assemblages. Kendeigh (1954) and Duellman (1965) reviewed methods used in interpreting faunal assemblages and discussed the limitations inherent in these concepts. The Life-Zone Concept of Merriam (1890, 1894) was envisioned as a latitudinal transcontinental belt or vertical zonation belt in mountainous areas which incorporated faunal and floral information with additional climatic data, particularly temperature. The Life-Zone Concept was used by Goldman (1951) and applied to the zoogeographic characteristics of Mexico in order to evaluate the distribution of birds, mammals, and the flora community. Stuart (1964) felt that Goldman's summary tended to reflect the Biotic Province Concept. The Biotic Province (Vestal 1914; Dice 1943, 1952) was defined by Duellman (1965) as ". . . a considerable and continuous geographic area that is characterized by the occurrence of one or more important ecological associations that differ, at least in proportional area covered, from the associations of adjacent provinces." Smith (1939), utilizing the lizard genus *Sceloporus,* attempted to map biotic provinces in Mexico. Later (1940, 1949) he modified his position concerning the application of the biotic province concept (see also Peters 1955). Smith (1960) noted, ". . . extensive agreement of range limits of numerous species is a necessary assumption in acceptance of the validity of the biotic province concept." It is unlikely that any two plant or animal species are affected identically by all environmental components; consequently,

no two species or subspecies can be expected to have identical ranges.

Bearing these difficulties in mind, we attempted to delineate the patterns of distribution of 42 taxa of Mexican rattlesnakes by consulting two faunal and two climatic assemblages: Life-Zone Concept of Goldman (1951), Biotic Province Concept (Stuart 1964), Temperature and Rainfall Provinces (Page 1930), and the Koeppen climatic classification system. The last system, outlined by Koeppen (1900, 1948), Koeppen and Geiger (1930-39) and summarized by Vivó (1964), roughly delineates the climatic types and utilizes data from annual and monthly averages of temperature and precipitation, including the variable effect upon plant growth through evaporation.

Frequency of occurrence for distributional overlap is presented in Table 1. Two taxa *(C. atrox, C. molossus nigrescens)* occurred in six Koeppen provinces. *Crotalus atrox* and *C. d. durissus* inhabited six and five biotic provinces, respectively. Four Life-Zone Provinces were applicable to *C. t. triseriatus. Crotalus molossus nigrescens* and *C. s. scutulatus* occurred in five rainfall provinces, and *C. atrox* inhabited five temperature provinces.

The validity of physiographic, climatic or biotic provinces, at least when used to explain the distribution of rattlesnakes in terrain as complex physiographically as Mexico, is highly tenuous. The discrepancies failed to produce an explanation of distribution that can be considered to be either valid or useful. Hence, an analysis of the ecological requirements of rattlesnakes must be concerned primarily with the microhabitat or habitat niche (Dammann 1961).

Food. Our field experience suggested that the occurrence of montane rattlesnakes in a given habitat was related to the availability of members of the lizard genus *Sceloporus*. The density of rattlesnake populations was considerably greater when an area supported a large number of lizards, especially species of *Sceloporus* which are largely saxicolous. We suspect that the feeding patterns of the smaller montane rattlesnakes are correlated with the diurnal

TABLE 1. Frequency of occurrence for distributional overlap in 42 taxa of Mexican rattlesnakes according to biotic or climatic classifications. Percentage followed by number of taxa in parentheses.

	Number of Biotic or Climatic Provinces In Which Taxa Occur					
Classification System	*1*	*2*	*3*	*4*	*5*	*6*
Temperature (Page 1930)	67(28)	24(10)	5(2)	0(0)	5(2)	0(0)
Rainfall (Page 1930)	50(21)	19(8)	21(9)	5(2)	5(2)	0(0)
Life-Zone (Goldman 1951)	74(31)	19(8)	5(2)	2(1)	0(0)	0(0)
Biotic Province (Stuart 1964)	52(22)	19(8)	21(9)	2(1)	2(1)	2(1)
Climate (Koeppen 1900, 1948)	33(14)	33(14)	14(6)	12(5)	0(0)	7(3)

activity patterns of various species of *Sceloporus*. On one occasion in the early afternoon at Llano Grande, Durango, a *Sceloporus poinsetti* darted from a clump of rocks and died a few minutes later. After five minutes, an adult *C. p. pricei* emerged, trailed the lizard and consumed it.

Captive *C. pricei, C. intermedius, C. lepidus, C. triseriatus,* and *C. willardi* showed a marked preference for lizards rather than rodents. The snakes usually struck the lizards in the thoracic region and held onto them until movement ceased. When rodents were struck, they were, in most cases, released. Captive juvenile examples of the larger lowland rattlesnake taxa preferred appropriate sized laboratory mice.

Ritualized Male Combat. *Crotalus atrox, C. intermedius gloydi, C. i. omiltemanus, C. lepidus klauberi, C. pusillus, C. t. triseriatus, C. t. aquilus,* and *Sistrurus ravus* engaged in ritualized male combat in captivity. A detailed description has been published for *C. lepidus* (Carpenter *et al.* 1976) and a comparative analysis of the other taxa will be forthcoming (manuscript in prep.).

Courtship and Mating Behavior. The following Mexican rattlesnakes were observed engaging in courtship and/or mating behavior in captivity: *Crotalus atrox, C. catalinensis, C. durissus culminatus, C. d. tzabcan, C. durissus* ssp., *C. e. enyo, C. intermedius omiltemanus, C. l. lepidus, C. l. klauberi, C. l. morulus, C. m. mitchelli, C. m. muertensis, C. molossus nigrescens, C. p. pricei, C. pusillus, C. t. triseriatus, C. t. aquilus, C. w. willardi, C. w. amabilis, C. w. silus,* and *Sistrurus ravus.*

The general pattern of courtship and copulation is summarized in the following account. Shedding by the female often stimulated male courtship activity and the female frequently defecated, presumably to evacuate the cloaca. The male directed head-bobbing and tongue-flicking sequences upon the head and dorsum of the female. If the female was in a resting coil, the male might vigorously press his lower jaw against her body in order to stimulate her to crawl. This action allowed for alignment of the bodies. The head-neck angle of the male varied between 30-45° and the male's mental region was pressed on the female's dorsum. The dorsal advance movements by the male, either sagittally, para-sagittally or laterally, included a head-bobbing motion which varied interspecifically from no lateral movement to a pronounced side-to-side motion. Female *C. atrox* assumed a raised head and anterior trunk stance on occasion; possibly this was a rejection posture (manuscript in prep.). As the male directed courtship activities toward the female, she raised her tail and gaped the cloaca (as in *C. atrox, C. d. durissus, C. pusillus*) which often stimulated the male. The male encircled the female's tail with his tail and rapidly slid his caudal configuration in anteriorly and posteriorly directed movements (as in *C.*

durissus tzabcan, C. d. durissus, C. e. enyo, C. pusillus). This behavior has been termed the "stroke-cycle" (Chiszar *et al.* 1976). The male draped large-radius coils over the female's body and attempted to place the cloacae in apposition by sliding his tail under the tail of the female. The male might push backwards against the resistance of the female's tail as he inserted (as in *C. d. durissus, C. pusillus*). Only one hemipenis was inserted, and eversion of the hemipenis prior to insertion was never observed. The tactile-chase and tactile-alignment patterns varied from 4 minutes in *C. willardi* to over 3 hours in *C. pusillus.* The range of variation might be due to female receptivity. Coitus varied from 2 hours in *C. atrox* to 9 hours in *C. w. willardi.* Jerking and twitching generally ceased when intromission occurred, but often the male maintained a steady pulsation of the body near the tail (as in *C. atrox, C. pusillus*). The female might drag the male backwards by the attached hemipenis (observed in *C. atrox, C. d. durissus*) until separation occurred.

Reproduction. The rainy season in Mexico usually occurs between May and October, and the dry season between December and April. In parts of southern Mexico, a short dry season occurs during the summer rainy period. During late June and early July, the rainy season normally begins in northern Mexico. In late July and September, the rainy season starts in central and southern Mexico. The northwest area of Baja California receives winter rains whereas the southern section receives summer rains.

In compiling literature references and our observations on parturition in wild Mexican rattlesnakes, we accumulated the following data on broods: 11 litters were born in June, 12 in July, 16 in August, 2 in September, 1 in October, and 1 in January. Compiled observations on our captive individuals revealed 5 litters born in June, 4 in July, 8 in August, 4 in September, and 1 in October. Data on these rattlesnake taxa are listed in Table 2. Parturition in Mexican rattlesnakes studied to date coincides with the rainy season, possibly due to a greater abundance of potential food items available at this time.

Warning Mechanisms and Defensive Actions. In addition to the use of the rattle as a warning mechanism and the striking coil, a number of other defensive behaviors were observed by us in Mexican rattlesnakes. When seized by collecting tongs, many of the smaller montane taxa turned and bit in lieu of assuming a striking coil. Some, especially *C. intermedius*, began spinning on a longitudinal axis. Adult *C. durissus tzabcan* raised the anterior portion of the body in an almost vertical column with a lateral bend in the neck, and faced the intruder. Captive juvenile *C. d. tzabcan* flattened and rotated their head and cervical region as much as 90° so that the dorsal aspect, with the contrasting pattern

on the head and the dark paravertebral neck stripes, was visible. Young captive *C. durissus totonacus* inflated their trunk, exhibited convulsive movements and, on rare occasions, flipped over upon the dorsum when confronted by a human observer. *Crotalus polystictus* usually thrashed wildly with pronounced lateral undulations when handled; this snake sometimes returned to a striking coil when cornered. An adult *C. s. scutulatus* and some examples of *Sistrurus ravus* repeatedly flattened their heads and trunks on the substrate, then lifted the tails vertically and waved them slowly in response to the presence of humans. The snakes did not attempt to rattle. Some of the smaller rattlesnakes responded to the presence of live mice and rats by launching into a striking coil, then struck the rodents with closed mouth. Rattlesnakes reacted to kingsnakes and other ophiophagous snakes by forming pronounced body-bridges which were used to strike the predators. Dermal substances of ophiophagus snakes elicited body-bridging responses from a number of Mexican rattlesnake taxa (Weldon and Burghardt, 1979). *Crotalus tortugensis*, when touched, used vertical body-bridges or lateral flexures to strike an annoying object. Frequently, the force was great enough to knock freshly killed rodents from the feeding forceps.

Crotalus stejnegeri vertically elevated its tail and a portion of the posterior trunk and held them rigidly as it assumed a striking coil. Although Klauber (1956) was unaware of an open mouth

TABLE 2. Data on rattlesnake litters with viable young showing number of young, length of young, and weight of young. Numbers in parentheses are means.

Taxon	*Number of young*	*Total length (mm)*	*Weight (g)*
C. atrox	6–25(14.3)	–	–
C. durissus ssp.	10	–	–
C. d. tzabcan	21	290–350(316)	18.4–26.8(23.4)
C. e. furvus	7	206–222(213)	–
C. intermedius omiltemanus	5	194–212(205)	4.9– 5.4(5.2)
C. l. lepidus	6	165–190(177)	5.0– 5.7(5.2)
C. l. klauberi	3– 5(4)	181–196(191)	6.3– 7.0(6.6)
C. l. morulus	4	–	–
C. m. mitchelli	1	275	17.5
C. m. muertensis	4	143–179(167)	3.3– 7.0(4.9)
C. molossus nigrescens	5	291–316(304)	25.4–27.4(26.6)
C. polystictus	5–12(8)	155–287(214)	2.4–11.5(8.9)
C. p. pricei	3– 9(5.3)	152–185(164)	2.7– 5.6(4.1)
C. p. miquihuanus	4– 5(4.5)	130–143(135)	2.6(2.6)
C. pusillus	3– 5(4)	165–179(171)	3.0– 6.1(4.0)
C. t. triseriatus	4– 6(5)	159–178(168)	4.8– 5.1(4.9)
C. t. aquilus	2– 7(4.7)	120–192(168)	4.9– 8.8(6.1)
C. willardi silus	4– 5(4.5)	146–218(190)	4.9– 6.9(6.0)
Sistrurus ravus	3– 9(6.3)	160–208(183)	3.9– 7.4(5.4)

threatening posture in rattlesnakes, three *C. molossus nigrescens* observed by us repeatedly exhibited this behavior for periods as long as five minutes. One *C. polystictus* also assumed this posture.

Crotalus atrox, C. lepidus, C. molossus, C. scutulatus, and *Sistrurus ravus* emitted musk upon capture. An adult *C. durissus* discharged a stream of musk while being restrained.

RESUMEN

Se presenta información sobre la ecología e historia natural de 45 taxa de cascabeles mejicanos, generos *Crotalus* y *Sistrurus*.

Observaciones de la fisiografía, geología, clima, y la vegetación de México son registradas en lo que se refiere a los cascabeles de esa región. Datos de observaciones tomadas directas de poblaciones naturales y ejemplares captivos son listados, incluyendo los predilecciones de habitación, extenciones de area y elevación, reprodución, periódos de actividad, y comportamiento.

La mayoría de los cascabeles monteses habitan bosques de pino y encino, llanos cubierto de hierba, y desiertos de altura. Generalmente los afloramientos rocosos son un factor determinante. Algunas taxa de tierra baja se encuentran en bosques tropicales áridos con afloramientos rocosos. Refugios específicos son a menudo utilizados por cascabeles monteses. Microhabitaciones con orientación hacia el sur son habitadas con mas frequencia por cascabeles de los altos, sequido por el sudeste, este, norte, noreste, y oeste en el orden de preferencia. Casi todas las taxa monteses se encuentran a 1800 metros o más de altura. Una distribución limitada en elevaciones relativamente bajas caracterizan la habitación de *Crotalus stejnegeri* (y talvez *C. lannomi*). *Sistrurus ravus* es una excepción ya que este se encuentre en asociaciones variadas. El grado de inclinación de la falda es importante. La densidad de la vegetación va de leve a moderado.

Rayos del sol difusos y alta humidad atmosférico contribuyen a la actividad diaria, especialmente en las culebras que habitan regiones montañosas. Especies de tierras altas tienden a ser diurnas y las de tierras bajas nocturnas, especialmente en el verano. Treinta dos taxa fueron encontrados activas durante el día y diez y ocho fueron cazadas de noche. Serpientes adultos *(C. intermedius, C. lepidus, C. triseriatus)* pueden permanecer en el mismo lugar por lo menos dos semanas y utilizar la misma peña para tomar el sol. Ejemplares juveniles de estas taxa fueron encontradas de noche.

La actividad de cascabeles en México depende de la epoca lluviosa. Pocas culebras se encuentran durante la epoca seca.

Los patrones de distribución de cascabeles mejicanos no se explican por uso de asambleas faunales ni climáticas. La frecuencia de traslape distribucional involucraben tanto como seis provincias

faunales o climáticos para una forma de cascabel. Estas discrepencias sugieren que los requisitos ecológicos de los cascabeles tienen que ser primariamente evaluados con un análisis de microhabitación o nicho habitacional.

La ocurrencia de las culebras montaneses se relaciona, en parte, a la disponabilidad de especies de *Sceloporus*. Muchas de las culebras pequeñas de altura muestran una decidida preferencia por lagartijas como comida y las cascabeles jóvenes de tierra baja prefieren roedores pequeños.

Combate ritualizado entre machos fue observado en *C. atrox, C. intermedius gloydi, C. i. omiltemanus, C. lepidus klauberi, C. pusillus, C. t. triseriatus, C. t. aquilus* y *Sistrurus ravus*.

Los aspectos de cortejo y/o brama fueron registrados en diecinueve distintas cascabeles captivos. Un patrón generalizado de comportamiento fue aparente y esta descrito.

Parturación en los cascabeles mejicanos estudiados hasta la fecha coincide con la epoca lluviosa. Información reproductiva de 19 taxa es presentada.

Comportamiento de advertencia, adicional al enrollamiento, ataque, y resonamiento, incluye lo siguiente: torneando y mordiendo, rotando en su axis longitudinal, rotación de la cabeza y cuello, elevación vertical del cuerpo anterior, inflación del cuerpo, movimientos convulsos, aplastamiento en el suelo y undulación lente de la cola, lanzando con boca cerrada, amenanza con boca abierta, elevación vertical rigida de la cola y emision de almizcle.

APPENDIX

Range or altitude extensions for Mexican rattlesnake taxa reported in text.

Crotalus b. basiliscus	MICHOACÁN: near Dos Aguas in the Sierra de Coalcomán (2225 m)
Crotalus basiliscus oaxacus	OAXACA: 35.5 km NW Telixtlahuaca
Crotalus durissus culminatus	MICHOACÁN: 7 km W Morelia
Crotalus durissus totonacus	TAMAULIPAS: 20.8-48 km N Soto la Marina
Crotalus i. intermedius	PUEBLA: near Cacaloapan
Crotalus intermedius gloydi	OAXACA: near Cerro Machín (Sierra de Juárez), Suchixtepec (Sierra de Miahuatlán)

Crotalus intermedius omiltemanus	GUERRERO: 1.6 km SW Filo de Caballo, San Vicente, 1 km N Puerto del Gallo
Crotalus lepidus morulus	NUEVO LEÓN: 24-32 km NW Galeana
Crotalus stejnegeri	SINALOA: Ejido Tebaira
Crotalus triseriatus aquilus	HIDALGO: El Chico (3110 m)
Sistrurus ravus	GUERRERO: mountains of Central Guerrero

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